

Species of Zooplankton as a Means of Identifying Different Surface Waters and Demonstrating Their Movements and Mixing

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"IN AN AREA where several water bodies mix . . . the plankton animals alone can give the clue as to the water's origin unless the salinity differences are marked." Russell (1935) makes this statement during discussion of the indicator species *Sagitta elegans* Verrill and *S. setosa* J. Müller from the English Channel and southern Irish Sea, and he has shown that when the two species occurred together, they were indicative of mixed waters. The remark suggests the possibility that more general use could be made of zooplankton organisms to indicate the origins of the waters in an area of mixing.

Russell's investigations concerned an area already comparatively well known faunistically and hydrologically, which is not true of the waters about New Zealand. A means has been needed whereby indicator species can be selected and utilized to demonstrate the sources, movements, and mixing of the waters for such little known areas. Two recent developments have assisted the realization of this. First, Miller (1950) used the temperature-salinity (T-S) diagram to show the origins and interrelationships of the several waters contributing to a mixture over an area of the continental shelf near Cape Cod. Second, Pickford (1946, 1952) has shown that the occurrences of the squid *Vampyroteuthis infernalis* Chun, when related (in the conventional T-S diagram) to the temperature and salinity at its points of capture, are confined in certain water masses. Similarly Haffner (1952) and David (1955) demonstrate environmental control over the distributions re-

spectively, of several species of the bathypelagic fish *Chauliodus*, and of the chaetognath *Sagitta gazellae* Ritter-Zahony. An important corollary of this latter method is that representatives of the fauna of a water mass may be selected as indicators of the water through the relationships demonstrated to temperature and salinity.

The investigation by Miller concerned waters entering near-coastal areas; that of Pickford, and others, has been concerned with relating occurrences of species to particular oceanic water masses. By combining relevant procedures from the two techniques it would be reasonable to expect that the occurrences of zooplankton organisms could be viewed in relation to the waters entering, and in, a coastal area. Data from collections of plankton, temperatures, and salinities could then be evaluated in three general and related ways. From the combined diagrams it should be possible to identify a water body entering a particular locality, to select species which are representative of the fauna inhabiting that water, and to pursue the subsequent history of that water both from its own distribution and from the distributions of the selected species.

These several possibilities are investigated in the following account from data collected in oceanic and coastal waters, and their mixtures, about southern and eastern South Island, New Zealand. The collections are typical of those of many small scale surveys, but they were not intended for the present purpose and, therefore, are not ideal in certain respects. However, they do in fact demonstrate that the several possibilities may be realised.

The combined temperature-salinity and plankton (T-S-P) diagram is believed to con-

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tribute towards an objective determination of the indicator species in an area as comparatively little known as that about southern New Zealand. Further, the distribution of the species in the diagram can be used to confirm the distribution of the different waters. Salinity and temperature changes may take place over shorter, or longer distances, but may not be readily related to variation in the plankton occurrences. In the T-S-P diagram both physico-chemical changes in the environment, and the response to these of planktonic organisms, are demonstrable.

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MATERIALS AND METHODS

The collections of this study were made during surveying operations of H.M.N.Z.S.

"Lachlan" during January, February, and March, 1951. Stations were occupied between Wellington and the Auckland and Campbell islands (Figs. 1, 2), and data are from surface samples. Temperatures and salinities have been obtained for all stations; in addition, temperatures were usually taken at regular intervals between stations. Salinities and temperatures of subtropical water have been included from a cruise between Wellington and Auckland via the west coast of North Island (small, open circles in Fig. 3 and see pp. 21-23).

The temperature and salinity data from the above sources have been used to construct the T-S diagram (Fig. 3). All stations are included. Those for which only physico-chemical data are available are differentiated from those at which plankton tows were made as well.

Surface plankton collections were made at 65 of the stations (see Table 4). Hauls were of three minutes' duration, and procedure and gear were carefully standardised (Bary, in press). Samples have been analysed quantitatively and the order of abundance of the selected species has been entered on Figures 5 to 10. The quantitative treatment is of value, but its importance is reduced in the present study since samples were taken at varying times in the 24-hour period (see p. 19).

A scale of smaller increments than is usual in reporting on quantitative plankton analyses has been used in this study. They have been adopted because the short hauls frequently resulted in only small numbers of organisms being captured (see Table 4). It was necessary that occurrences of species in these small catches be adequately distinguished in order to detect whether there were reactions of species to changed environmental conditions and if these might be of ecological value.

Stations can be grouped conveniently into several series, as they were occupied during individual cruises (Series 4, 5, 6, and 7) or, failing this, in a particular area (Series 1, 2, and 3). In general, a series is spread over a

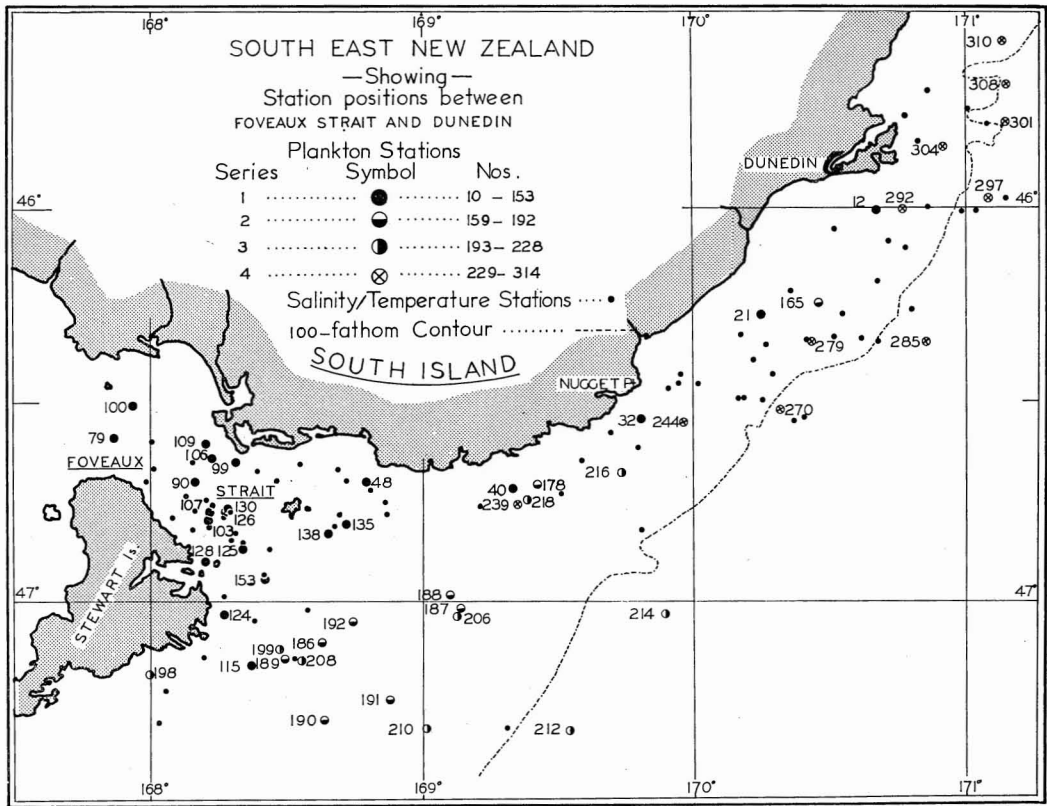


FIG. 1. Temperature/salinity and plankton stations in and about Foveaux Strait, southern New Zealand. Only plankton stations are numbered.

few days except for Series 1, in which stations accumulated irregularly over a period of 18 days; however, the stations are mostly from Foveaux Strait (Fig. 1). Information about the series is summarised in Table 1. In Figures 1, 2, and 3, each series of stations is symbolised separately; in subsequent figures this has not been practicable and for these it is necessary to locate stations in Figures 1, 2, or 3.

The method develops in two stages. In the first, each species is plotted, showing the order of its abundance, in the intercept of the salinity and temperature for all stations at which it was taken. In effect, species occurrences are superimposed on the T-S diagram to produce the temperature-salinity-plankton (T-S-P) diagrams (Figs. 5-10; note that the scale of Figs. 3 and 10 differs from that of

Figs. 5-9). The correlations of species and water properties thus demonstrated, together with previous distributional records of the species, have enabled species to be selected which occur consistently within those ranges of properties typifying certain water bodies. These species are indicator species, and 25 have been selected. They form into four separate groups (Tables 3, 4), each of which is considered to represent the planktonic population normally associated with a particular range of environmental conditions. Figure 10 summarises the interrelationships of these four groups. In the second stage, the distribution of each group in the T-S-P diagrams is correlated with the geographic distributions of both the group and properties of the waters. In this way, those similarities and differences of the planktonic content between sta-

TABLE 1
THE STATION SERIES, THEIR LOCATION, AND PERIODS OF OPERATION

SERIES NO.	STATIONS NOS.	DATES	NO. OF DAYS	GENERAL LOCALITY OF STATIONS
1.....	10-153	5-6 to 24.I.51	18	} Foveaux Strait and southeastern New Zealand
2.....	159-192	29.I to 1.II.51	3	
3.....	193-228	5 to 13.II.51	8	
4.....	229-314	8 to 9.III.51	1	
5.....	1-6	3 to 4.I.51	1	} Between Wellington and Dunedin
6.....	320-343	21 to 22.III.51	1	
7.....	795, 826, 921	13 to 17.XI.51	4	Between southern New Zealand and Auckland-Campbell islands

tions or groups of stations in the T-S-P diagrams, are considered geographically in relation to the distribution of the water properties which result from the movements of water bodies relative to one another.

SOME GENERAL CONSIDERATIONS

Either the method proposed in this study, or that adopted by Pickford, may be used to select those species which are indicative of oceanic water masses. An alternative use of the present method is to select those species which are indicative of the environmental conditions in a particular, restricted, and little-known area. However, in a wider survey, one or more of these same species may be found in such a variety of conditions as to render them valueless as indicator species. Most of the indicator species in the present study are regarded as useful throughout the area considered, but it might well be necessary to select other indicators for a locality with hydrologic conditions dissimilar to those found in the eastern and southern waters of New Zealand.

The occurrences of two species in the present survey illustrate these remarks and, at the same time, demonstrate the feasibility of using species other than those which previous information would suggest as suitable indicators for the waters in the area. *Thysanoessa*

gregaria Sars is a tropical-subtropical-cool-temperate euphausiid which occasionally occurs in subantarctic waters (Sheard, 1953; Boden, 1954). However, it occurred as a breeding population in this survey, sometimes in high numbers, between the southern Auckland and Campbell islands and the subtropical convergence, i.e., in waters believed to be of subantarctic origin. *Cylopus magellanicus* (Amphipoda) and *Eucalanus acus* (Copepoda) have similar distributions and are typical subantarctic species (Barnard, 1930; Farran, 1929). *Paracalanus parvus* is a widespread copepod (Wilson, 1932; Vervoort, 1949). Brady (1915) recorded it as "fairly common" to 64° 34.5'S. (in 127° 08' E. long.) and at Auckland Island. In the present study, *P. parvus* occurred consistently, in large or very large numbers, in water believed to have originated in the subantarctic and become warmed in its progress northward. It was associated with *Euphausia lucens*, which is recognised as inhabiting warmer northern subantarctic waters (John, 1936), and with *Sagitta serratodentata* var. *tasmanica*, a "cold-tolerant" species (Thomson, 1947, and see p. 31). A few other species, e.g., among the Amphipoda, could be discussed similarly. These are species for which previous distributional records are at variance with the usage in this survey. However, it can be demon-

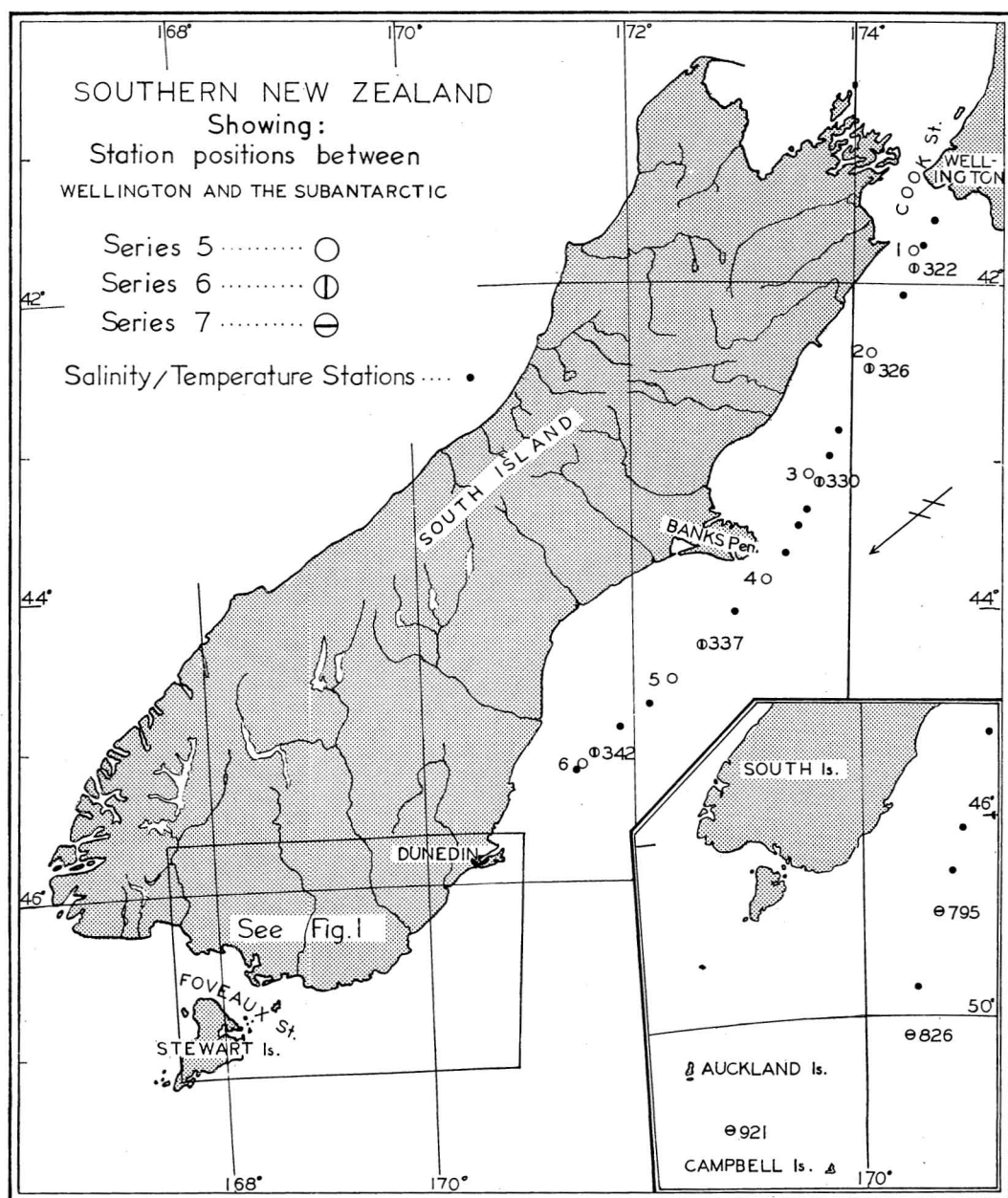


FIG. 2. Temperature/salinity, and plankton stations between Wellington and Dunedin in January (1-6), and March (320-343), 1951. The arrow shows the course of the ship which took the surface thermograph trace in Figure 4b. The approximate position of the subtropical convergence is shown by the two bars crossing the shaft.

INSET: Temperature/salinity and plankton stations between southern New Zealand and Auckland and Campbell islands, November 1951.

Only plankton stations are numbered.

TABLE 2
GENERAL PROPERTIES OF WATERS IN THE SUBANTARCTIC, AND OFF EASTERN AND SOUTHERN NEW ZEALAND*

WATER BODY	SALINITY, ‰	TEMPERATURE, °C.
Of Subantarctic Origin		
i. cold subantarctic.....	34.0 to 34.3	8.2 to 10.9
ii. warmed subantarctic.....	34.3 to 34.7	11 to 13.0
Of Subtropical Origin.....	35.0 to 35.5	13 to 17.5 plus
Coastal.....	— up to 35	13 to 16 plus

* The values listed are derived from the present sampling, but they approximate those given by Deacon (1937) for waters of subantarctic and subtropical origins.

strated that for the particular local conditions, each is largely confined within certain ranges of salinity and temperature (except possibly where mixing is taking place), and that each occurs in conjunction with species which can be stated as undoubtedly resident in the water characterised by those properties. They are thus useful indicator species under the local conditions.

To cover the conditions which may occur in mixed waters it is necessary that indicator species are selected as far as possible to include a range of adaptabilities. To this end more than one species is desirable from each water body. Further, several species may provide additional information through their variable reactions. For example, an adaptable species may maintain an association with a mixture of particular waters whereas a less adaptable one would not.

Frequent short plankton tows, with corresponding numbers of hydrographic samples, might well provide a better index to the overall surface conditions in an area than fewer hydrographic samples and fewer, but longer, tows. The latter may increase the quantity of a catch, but may decrease the relative accuracy with which the biologic sample can be related to the physico-chemical conditions. This would apply especially where steep gradients may exist, as for example in mixing waters. The geographic distributions of indicator species selected from the three-minute tows of this survey are found to closely coincide with the geographic distri-

butions of their respective waters. This general accord suggests that, although surface tows may vary quantitatively and qualitatively between one time and place and another, the present procedures have largely met the requirements for this type of study.

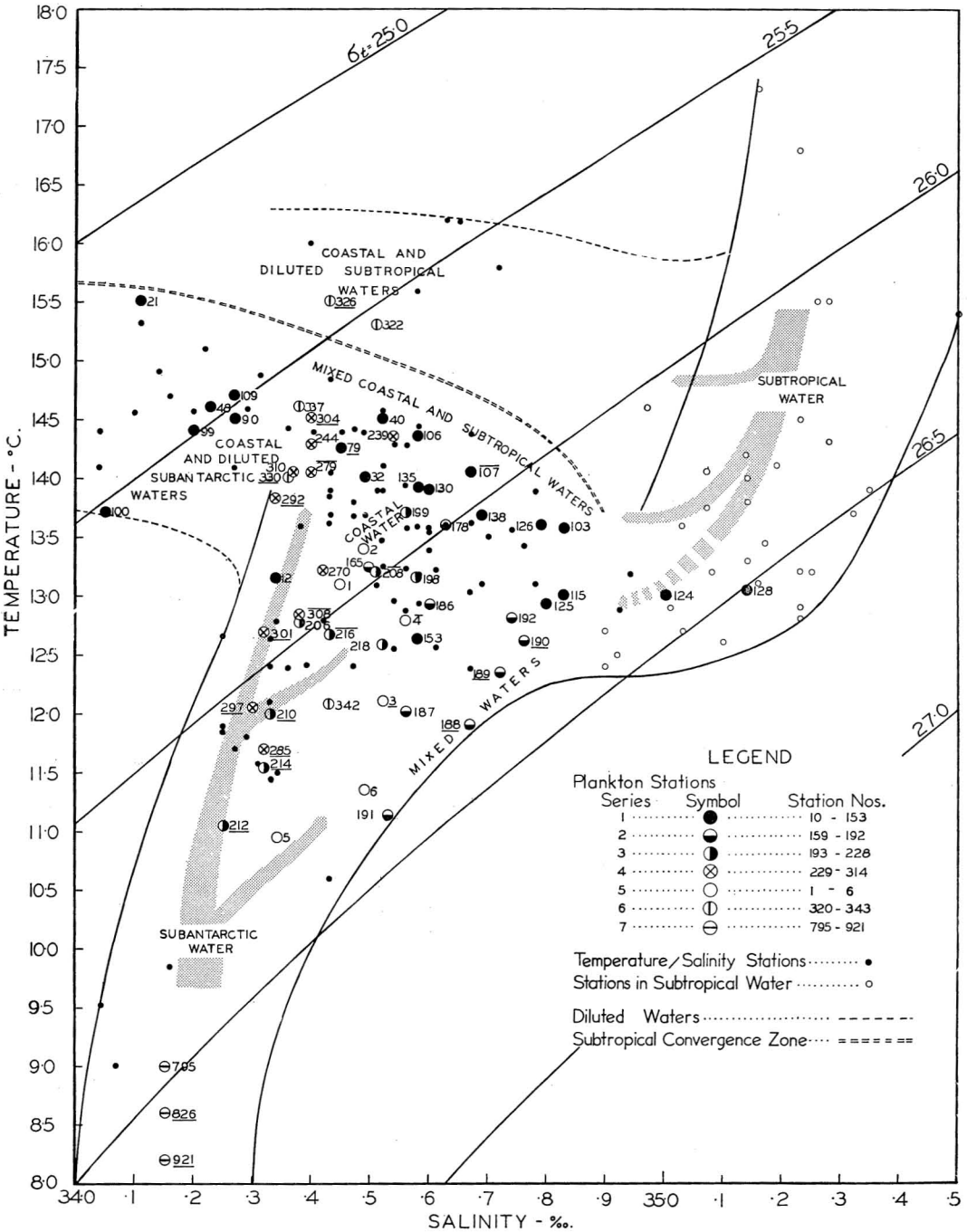
Collections were made as opportunity permitted. As a consequence two features possibly affect the distribution of species in the T-S-P diagrams, namely, diurnal migration of species and the asynoptic nature of the collections.

The effects of diurnal migration have been analysed in some detail. (Times of stations are given in Table 4. In this table, and in Fig. 3, stations are divided into those occupied during daylight, at night, and between dawn and sunrise, and between sunset and dark.) As would be expected, the numbers of species and of specimens captured increased at night (Table 4). It was thought that variations of this nature might render the T-S-P diagram of less value in the selection of indicator species, and, more especially, for reliably correlating their distributions with hydrological conditions. The fact that several species form an indicator group has some bearing. Thus, if the suspected adverse effects of diurnal migration on distribution were to be realised, all species of a group would have to react similarly at the one time. Occasions will arise when all species of a group could, for example, be absent from the surface at the same time. These occasions appear to affect group-distribution patterns in the diagrams

only in details, as discussed below.

The analysis has shown that all series of stations contained night tows and in all, except Series 1, at least some of these were con-

secutive. In addition, some species from the groups were captured in both day and night hauls. Two important facts were also demonstrated. First, fewer night than day tows are



needed to produce a T-S-P diagram from which the distribution of the species group can be related to the hydrological conditions. Second, and the more important, is that in the majority of instances, *those species which were taken in daylight occurred in similar conditions of temperature and salinity to the same species taken at night*. In other words, when a species was collected in day and night tows, it occurred almost only in the environmental conditions which were acceptable. This is reflected in the cohesion of the species' distributions in each of the groups in the T-S-P diagrams. Therefore, day tows serve to supplement night tows from a distributional point of view in the diagrams, and it is believed that data from both may justifiably be used in their construction. It has been found preferable to base interpretations of distributional relationships on the species' groups because diurnal migration may be affecting detail. To guard against the possible adverse effects which might accrue, it would be desirable to occupy future stations at comparable times, and preferably at night.

In T-S-P diagrams planktonic groups, or species, are shown independently of their times of capture. Therefore, occurrences of either individual species, or groups of species, can be directly related only to the environmental conditions in which they were captured, and to the species' composition at other stations. The species, and through them, the species' groups, will react to environmental changes (if of sufficient magnitude), but when these occur is not important in the T-S-P diagram. It is possible, therefore, to utilise asynoptically collected data in the T-S-P diagram. When species or groups of

species are considered in relation to the geographic distribution of the water properties then it becomes essential that as near synoptic series as possible are utilised. Nevertheless, it is believed that even for the T-S-P diagram, the nearer the approach is to synoptically made collections (as, for example, Series 4 to 6), the more reliable will be interpretations from the diagrams.

Pickford (1952: 209) has plotted the occurrences of *Vampyroteuthis infernalis* in relation to density as well as salinity and temperature. She quotes a suggestion that the distribution of this species is determined by its being "passively caught in a layer of constant density. . . ." Because of this suggestion, densities are plotted in Figures 3 and 10. It appears from Figure 10, however, that species may occur over a wide range of densities. It would appear, therefore, that this factor has little if any control over the distribution of surface zooplankton in the area of sampling.

WATERS INFLUENCING SOUTHERN AND EASTERN NEW ZEALAND

The surface waters are described as being of subtropical origin in the northern half and of subantarctic origin in the southern half of eastern New Zealand (Deacon, 1937; Garner, 1954). To the west, and lying north of an ill-defined subtropical convergence zone (Garner, *loc. cit.*) is Tasman Sea water. It is believed to move in an east-going drift towards New Zealand (Deacon, *loc. cit.*). On approaching the west coast of South Island the bulk of the water seems to be deflected northwards while some is thought to move southward and penetrate towards Fovéaux Strait and Stewart Island (Deacon, Garner).

FIG. 3. T-S diagram of surface waters, southern and eastern New Zealand. Stations at which plankton was collected are differentiated from those where only salinities and temperatures were taken. Stippled arrows indicate the direction of water movements within the diagram, as deduced from the distribution of properties and the form of the water envelope (and as later confirmed by the plankton distribution). An underlined station number, e.g., 212, indicates a night tow; an overlined station number, e.g., 216, indicates a station occupied at dawn or dusk. An unmarked station is one occupied in daylight.

NOTE: The shape of this diagram superficially resembles that of the area in which samples were taken, but it is not a reproduction of the geographic area in another form.

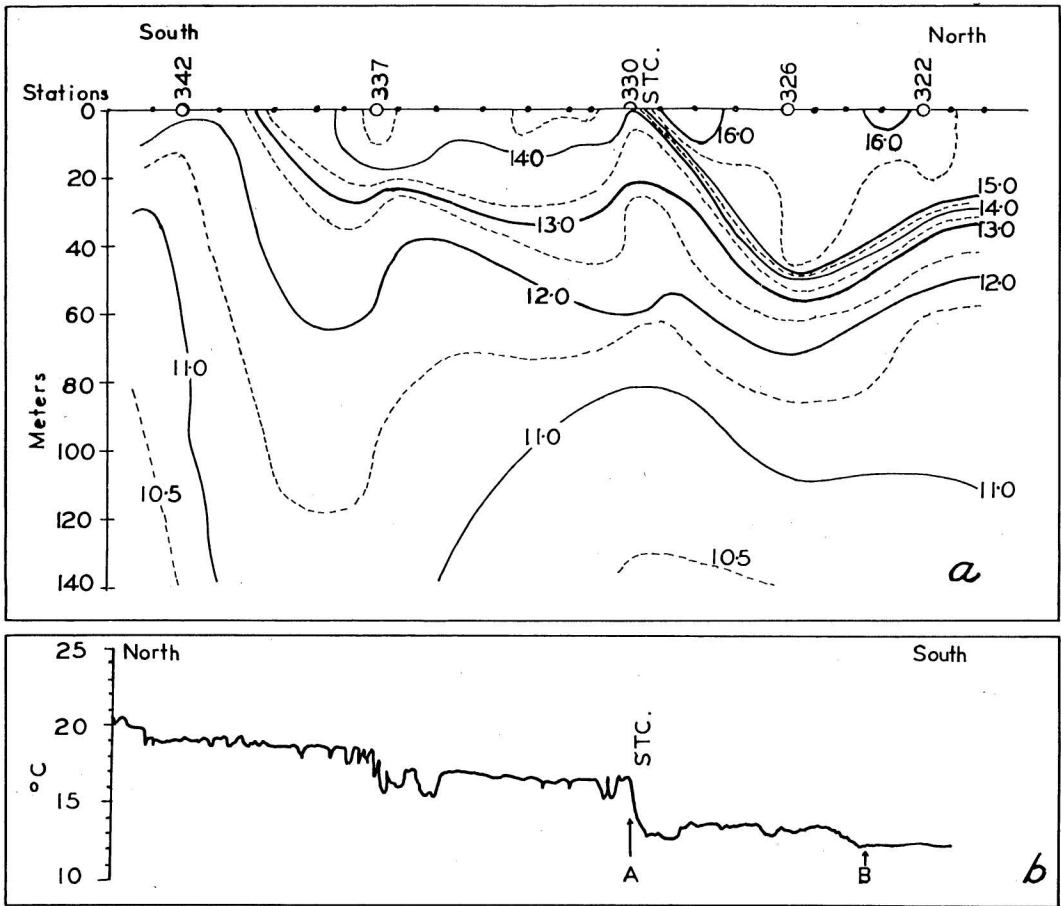


FIG. 4. *a.* Section to 140 m. between Wellington and Dunedin, March 21, 22, 1951. STC=position of sub-tropical convergence. Stations indicated by a circle are those at which bathythermograph casts were made; surface temperatures were taken at positions marked by dots.

b. Surface thermograph trace between 37° 32' S. and 178° 29' E. and Dunedin, mid-April, 1951. STC=position of sub-tropical convergence in 43° 24' S. 174° 34' E. (position A) distant 45 mi. and bearing approximately 96° from Station 330.

Few detailed data are available concerning the properties of the eastern central and southern Tasman Sea water.² That it is warmer and more saline than water of subantarctic origin is demonstrated by the temperatures and salinities of surface samples from the west of North Island between Wellington and North Cape (small open circles, Fig. 3). These data are of winter (July) conditions and consequently temperatures are low in comparison with the rest of the stations, which are summer stations. The temperature

ranges between 12.5° and 17.5°C. and the salinity between 35.0 and 35.5‰, values which are within those described for sub-tropical waters by Deacon (1937). For this

² Since this paper went to press, Rochford, D. J. (1957) has published an account of the waters of the Tasman Sea. He indicates that for the area west and south of South Island, New Zealand, subantarctic water exerts the main influence at all times. However, his data do not preclude the possibility that during spring and summer months some influence from warm Tasman Sea water (in part, my "water of sub-tropical origin") may penetrate southwards along the west coast towards Foveaux Strait. See his figure 25b.

TABLE 3
SPECIES' GROUPS, AS DETERMINED FROM THE
T-S-P DIAGRAMS, AND THE WATERS OF
WHICH THEY ARE INDICATORS

SPECIES' GROUP	WATER
Subantarctic	Water of Subantarctic origin
i. Southern Subantarctic species	from 8°C.
ii. Northern Subantarctic species	11°C. and higher
Subtropical Species	From, or due to, the influence of subtropical water
Coastal Species	Coastal water—an admixture of subantarctic, subtropical and fresh waters

reason, and for lack of any published evidence to the contrary, the Tasman Sea water and the waters northward of the subtropical convergence to the east of New Zealand are considered together as "water of subtropical origin" in this study. Whether in fact the physical and faunistic properties of the two areas will prove to be identical, or nearly so, has yet to be demonstrated. For the purpose of the present investigation the T-S characteristics of this water are included in Figure 3 for two reasons. First, they provide a contrast across the subtropical convergence with the water originating in the subantarctic; second, they delineate the mass from which the warm saline water (and a warm-water fauna) that influences southern and north-eastern South Island is being derived.

Subantarctic (West Wind Drift) water moves mostly toward the east, but with a northerly component. It has a strong influence on the waters of southern and eastern South Island (Garner, 1954) and perhaps also in some measure on those of the west coast. Some is also believed to pass into Foveaux Strait from the west. The temperature at Station 921 (Fig. 2) was 8.2°C., and it increases northwards to about 13°C. at the convergence. Salinity ranged between 34.0 and 34.3 ‰ in the colder waters and 34.3 and 34.7 ‰ in the warmer (northern) waters.

Such values are within those described for subantarctic water by Deacon (1937). The properties of these waters are summarised in Table 2 and their relationships illustrated in the T-S diagram, Figure 3.

Waters of subtropical and subantarctic origins meet in the subtropical convergence, a zone usually described as of variable width which is believed to migrate northwards in winter, southwards in summer. The existence of the convergence eastwards of New Zealand is undoubted, from evidence discussed by Deacon (1937) and Garner (1954). Evidence from the present survey indicates that it was crossed twice, with biological and hydrological samples being obtained during the first traverse. Data from surface waters from the cruise of March 21–22, 1951 (see Series 6, pp. 47, 48, and Figs. 4a, 19b, 20b), show that near Station 330 there was an abrupt increase northwards of 2°C. and of 0.3 to 0.4 ‰ salinity (over subantarctic salinities as at Stations 341, 342). The section constructed on the basis of bathythermograph records to 450 feet (approximately 138 m.) from between Wellington and Dunedin (Fig. 4a) shows that towards the north cool water was submerged beneath a layer 35 to 60 m. deep of warmer water. Immediately north of Station 330 this cool water reaches the surface. South of Station 330, and including Station 337, is a second body of warm water which is of coastal origin (Figs. 19b, 20b) and which overlies, and is mixing with, subantarctic water. On the second crossing on April 18, a surface thermograph trace (Fig. 4b) recorded a temperature drop from 16.8° to 12.8°C. in a position approximately 45 miles seaward on a bearing of 96° from Station 330 (Fig. 19b). These data are typical of those associated with a convergence of warm and cold waters, and it is believed they are attributable to the subtropical convergence. This would fit in with Garner's interpretation of these and other data, and, if so, the crossings herein discussed were of the southern extremity of a south-going tongue of subtropical water which was

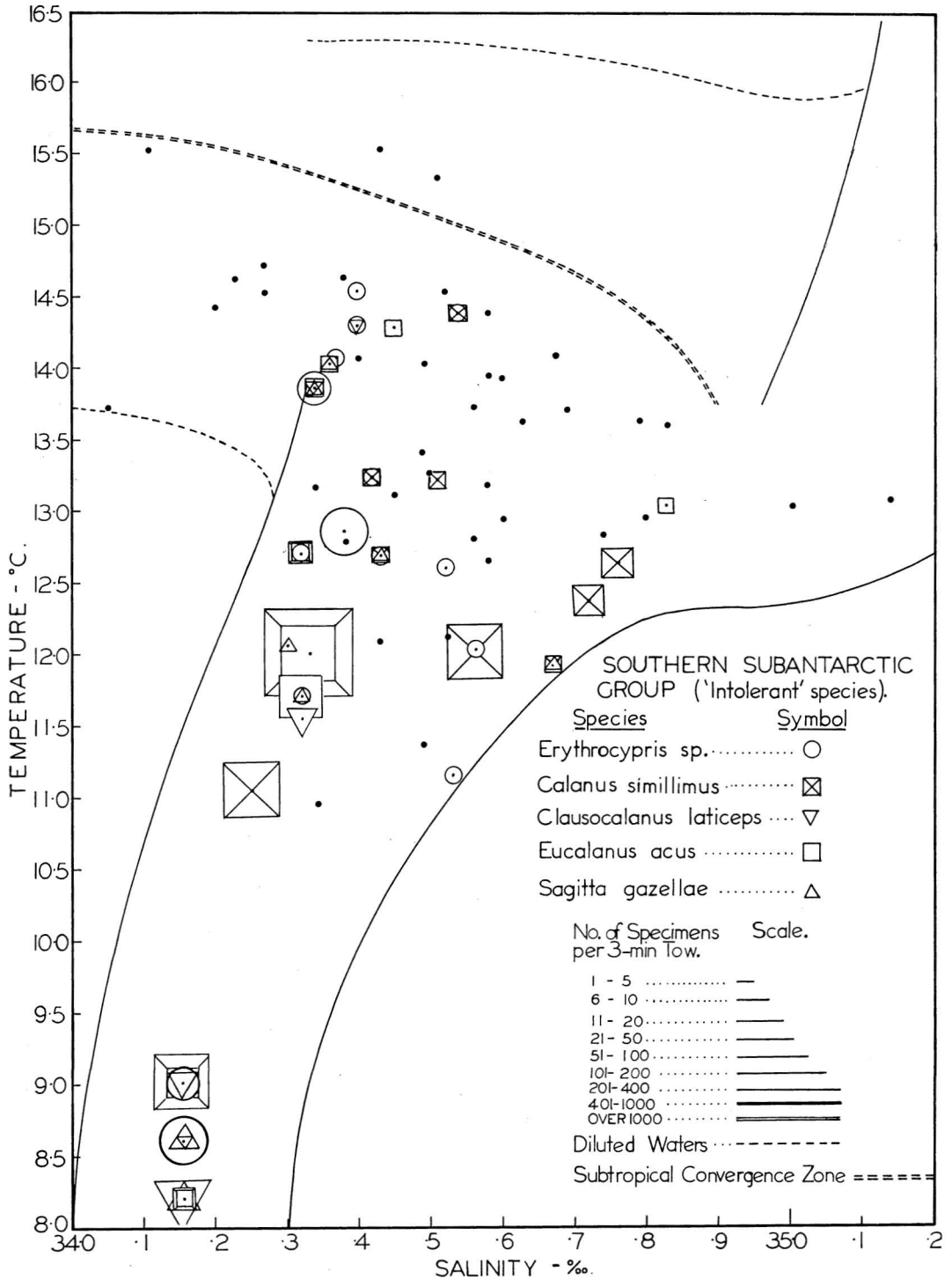


FIG. 5. The distribution in the temperature-salinity-plankton (T-S-P) diagram of Southern Subantarctic species which show a lack of adaptability toward coastal water through a marked reduction in the numbers taken from it. Water envelope as in Figure 3. Plankton stations at which no specimens were collected are shown by ●

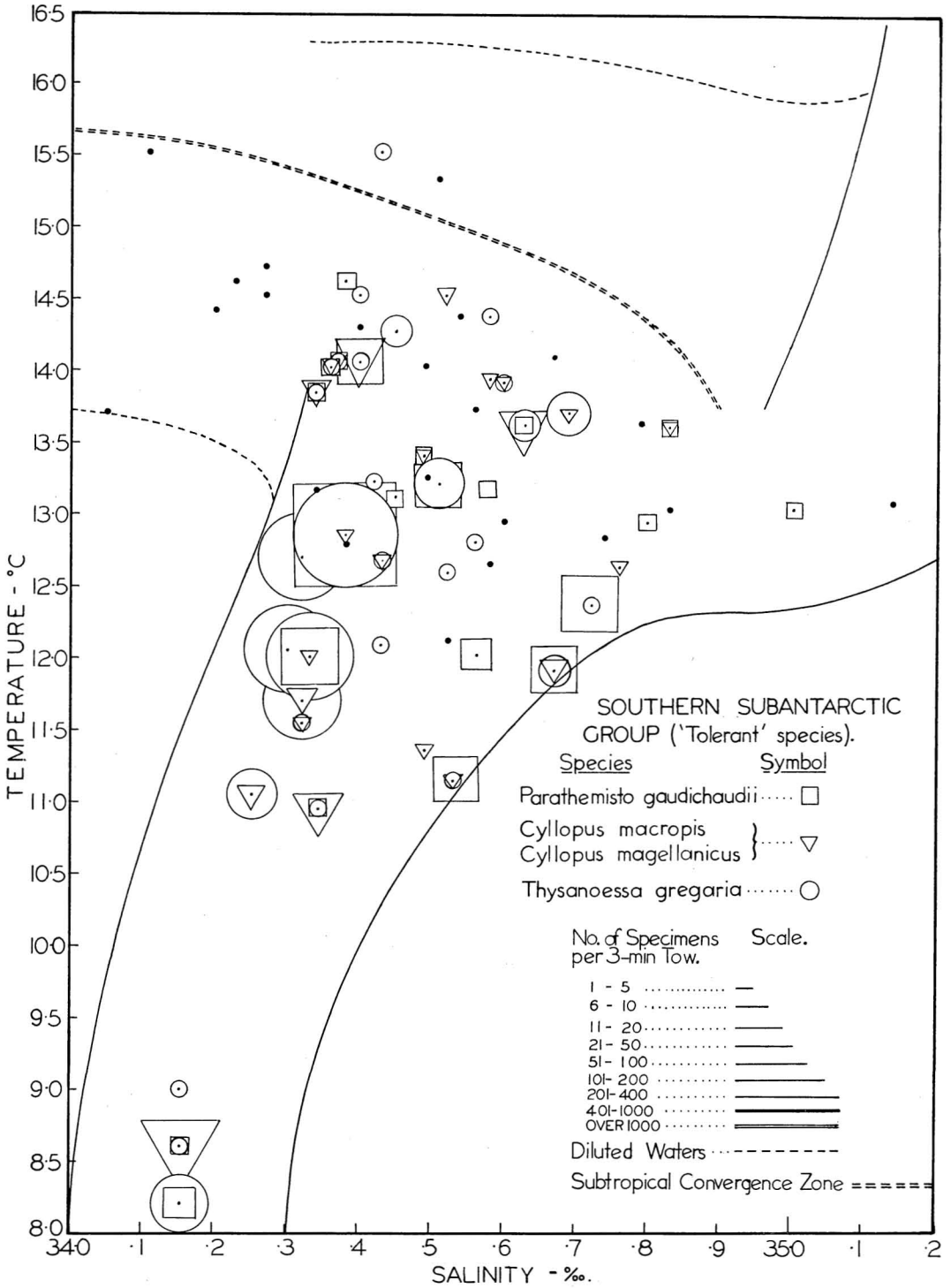


FIG. 6. The distribution in the T-S-P diagram of Southern Subantarctic species which are comparatively more widespread in (i.e., more "tolerant" of) coastal water. The numbers taken are higher in the coastal water than for the "Intolerant" species shown in Figure 5. Plankton stations at which no specimens of the group were taken are shown by ●

penetrating down the east coast—an extension of the East Cape Current (see Garner 1954, also his fig. 4*a*). That the data are in fact attributable to crossing the convergence is borne out to a considerable degree by the biological evidence.

Coastal water appears from Figure 3 to be an admixture of fresh water runoff and water of subtropical and subantarctic origins. Subantarctic water is of lower salinity than the water of subtropical origin and will dilute it; both of these waters and their mixtures will be diluted by fresh water. The salinity of coastal waters ranged from less than 34 ‰ (not shown in Fig. 3) up to about 35 ‰, and depends in part on which oceanic water predominates at a station, and on the proportion of fresh water in the coastal water mixture. The temperature ranged between 13° and 16°C., which is intermediate between those of waters of subtropical and subantarctic origins.

In the T-S diagram (Fig. 3) the water envelopes have been drawn arbitrarily to include all points entered. Solid lines indicate those water masses identifiable from the present data; dashed lines are indicative of dilution of the waters from these masses. The double dashed line signifies the subtropical convergence and separates all stations occupied to the south of it from those to the north. The proper extent of the convergence cannot be shown because the low winter temperatures of the water of subtropical origin permit the coolest samples from this water to be located in the summer temperature range of the coastal-subtropical mixture. Because of this, and because no stations crossed the convergence clear of the influence of coastal water, no position for the subtropical convergence between uncontaminated waters is shown in the diagram.

From the distribution of properties in the T-S diagram and from its form, general movements of both subtropical and subantarctic waters towards coastal water can be deduced. There will be mixing between these (and with fresh water) and this is represented in the

region of extreme salinity variation in the temperature range of about 13° to 15.5°C. Confirmatory evidence on water movements and especially those concerning mixing areas is to be derived from the distribution and interrelationships of the several groups of indicator species. In Figure 3, the stippled arrows show the general water movements as deduced from the T-S diagram, while in Figure 10 the movements as demonstrated by the planktonic distribution are illustrated. There is a general similarity.

SPECIES' GROUPS IN RELATION TO WATERS IN THE AREA

Four groups of species have been selected as representative of the zooplankton resident in the waters of the area of sampling (Tables 3, 4). There is one group from each of the coastal and subtropical waters, and two from water originating in the subantarctic. One of the subantarctic groups represents those species occurring predominantly in the colder waters and for convenience called the "Southern" Subantarctic Group; the other has been selected from those species occurring in water of subantarctic origin which has been warmed in its progress northward, namely, the "Northern" Subantarctic Group (see pp. 31-33).

The species and the species' groups are listed in Table 4, together with the numbers of specimens captured and the stations at which they were taken.

The degree to which the association of species in each of the groups is maintained in their normal environment, and when they are carried into abnormal conditions, is summarised in Figures 5 to 9 and is discussed below.

Southern Subantarctic Group

Stations 795, 826, and 921 (Fig. 2) lie within the field of cold subantarctic water as defined earlier, and appear to be removed from the influence of water of subtropical

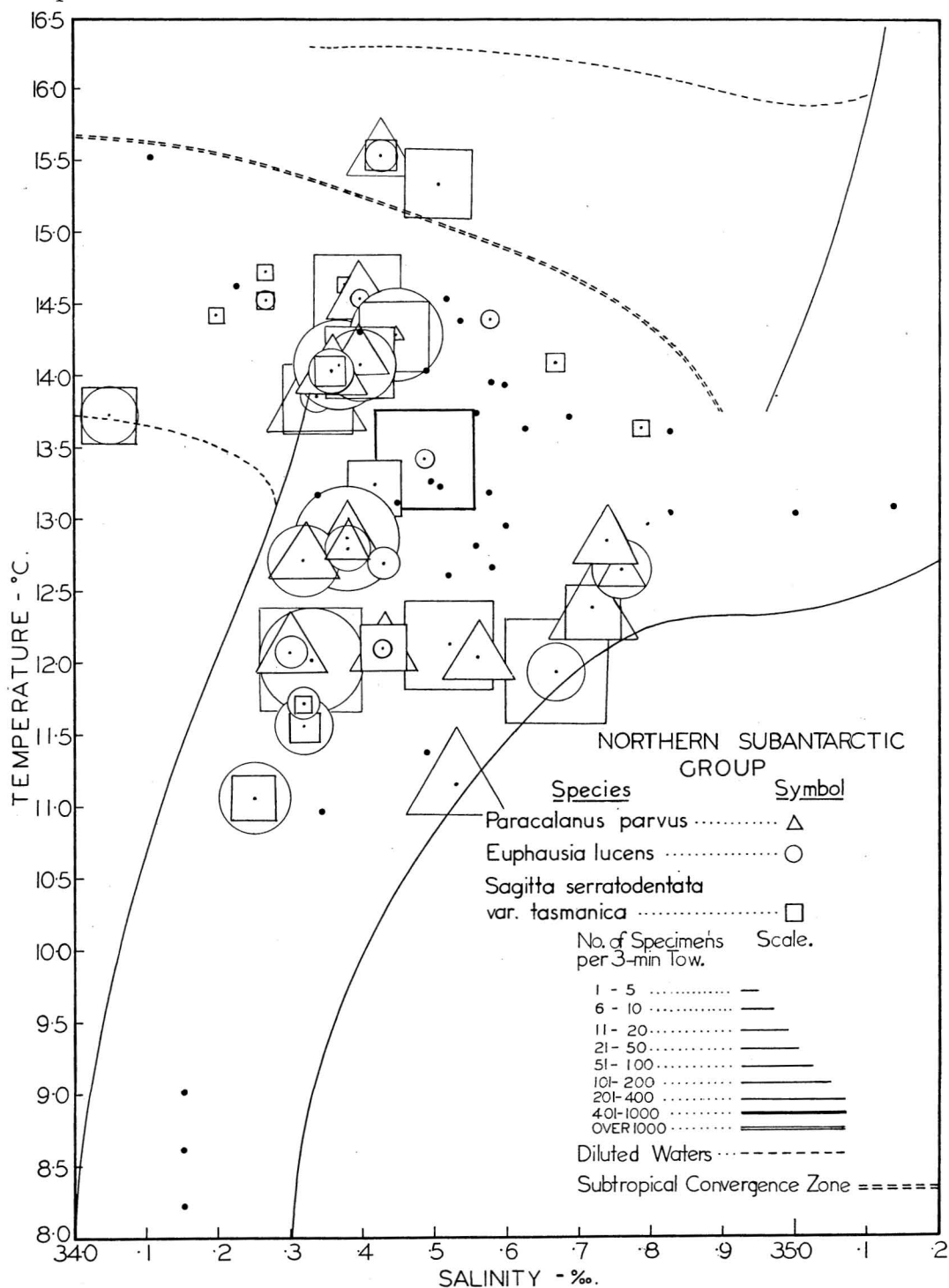


FIG. 7. The distribution of Northern Subantarctic species in the T-S-P diagram. Large numbers were taken. The species are confined to the northern, warmed subantarctic water, but extend into coastal water in strength in two areas where the subantarctic water is intruding into and mixing with, coastal water. Plankton stations at which no specimens of the group were taken are shown by ●

TABLE 4

[illegible]

TABLE 4 Continued
THE PLANKTON STATIONS, THEIR TIMES AND DATES, AND THE SPECIES AND GROUPS COLLECTED AT EACH

STATION NO.	TIME OF DAY † (HOURS)	SERIES		SOUTHERN SUBANTARCTIC							NORTHERN SUBANTARCTIC			SUBTROPICAL				COASTAL																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																											
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				<i>Erythrocypris</i> sp.																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									

TABLE 4 *Continued*
THE PLANKTON STATIONS, THEIR TIMES AND DATES, AND THE SPECIES AND GROUPS COLLECTED AT EACH

STATION NO.	TIME OF DAY† (HOURS)	SERIES		SOUTHERN SUBANTARCTIC								NORTHERN SUBANTARCTIC			SUBTROPICAL				COASTAL						
		Dates	No.	"Intolerant"					"Tolerant"																
				<i>Eurybrocpris</i> sp.	<i>Clausocalanus laticeps</i>	<i>Eucalanus acus</i>	<i>Calanus similimus</i>	<i>Sagittia gazellae</i>	<i>Parabemisto gaudichaudii</i>	<i>Cyllopus magellanicus</i>	<i>Cyllopus macrops</i>	<i>Thysanoessa gregaria</i>												<i>Paracalanus parvus</i>	<i>Euphausia lucens</i>
285	2200.N	8-9.III.51	4	2		16		3		8		67		6	5										
292	0015.N			7	1	2		1	1	10		3	288	8	55			243				1	249		
297	0205.N							3				200	100+	7											
301	0315.N			1		1	1					119	100+	87					6						
304	0423.N			1								1	100+	3	104				396						
308	0550.O			14					376	1		496	100+	236							10	24			
310	0630.D			3				5	1					115						1	15	3			
322	1630.D	21-22.III.51	6												55	165			1250			2	1		
326	2035.N											3	100+	6		31		11	826						
330	0030.N					1			3	1		5	100+	21	8						1			14	
337	0715.D								1						4									94	
342	1217.D										4	100+	4	14											
795	1900.D	13-17.XI.51	7	8	8	9	23					1													
826	0300.N			12	3			10	4	143		1													
921	0300.N				40	3	3	9	8			30													

* Combined totals of solitary and aggregate forms shown separately in Figure 8.

† D = daylight stations; N = stations at night; O = stations from dawn to sunrise, or sunset to dusk.

+ Signifies larger numbers of specimens than were counted.

origin. Species taken at these stations may be regarded as resident in such subantarctic water. Accordingly the species of the Southern Subantarctic Group have been selected from those collected at these stations.

Nine species have been selected. *Erythrocypris* sp., *Clausocalanus laticeps* Farran, and *Sagitta gazellae* Ritter-Zahony were present in small numbers, *Eucalanus acus* Farran in moderate numbers, and *Calanus simillimus* Giesbrecht was often very common, preponderantly as a Stage V copepodite. *Clausocalanus laticeps* and *E. acus* are both described as typically cold-water species (Farran, 1929; Hardy and Gunther, 1935) and stocks of *S. gazellae* are demonstrated as residing in antarctic and subantarctic waters by David (1955). *Calanus simillimus* is only to be captured from the southern waters (Vervoort, 1951). The numbers of these five species were noticeably reduced in coastal and mixed waters, which possibly indicates a lack of adaptability to the changed conditions. Consequently they have been distinguished as "Intolerant" species (Fig. 5). *Parathemisto* (*Euthemisto*) *gaudichaudii* (Guer.) and *Thysanoessa gregaria* Sars occurred commonly, but *Cyllopus macropis* (Bovallius) and *C. magellanicus* Dana were present in smaller numbers. *Thysanoessa gregaria* was discussed on page 17. *P. gaudichaudii* is a fairly widespread species in the colder waters of northern and southern hemispheres, while *Cyllopus* spp. have been recorded only from the colder southern waters (Stebbing, 1888; Barnard, 1930; Hurley, 1955; Hardy and Gunther, 1935). Larger numbers of these species penetrate into coastal waters, which suggests a greater tolerance towards altered conditions than was apparent among the "Intolerant" species; they are accordingly distinguished as "Tolerant" species (Fig. 6). Both "Tolerant" and "Intolerant" species belong in the Southern Group.

In the T-S-P diagrams Southern Subantarctic species are in continuous distribution, in moderate to high numbers, throughout water of subantarctic origin. All of the species

occur as well in coastal water, but the numbers of specimens collected decrease with modification of the environmental conditions as mixing progresses between the subantarctic and coastal waters. This is especially so of the "Intolerant" species. Dilution by fresh water (Stations 99, 90, 48, 109) and, to a lesser degree, increase in salinity (Stations 126, 103, 124) appear to restrict the "lateral" spread of species in the diagrams although much of their apparent effects may be due to the stations having been occupied in daylight. Rising temperatures are less restrictive. Most of the species were taken throughout the range sampled, but much less commonly at the higher temperatures, even in hauls made at night.

Transfers of species from subantarctic to coastal waters were largely concentrated about three groups of stations, namely 292, 330, 310, 304, 79, 40, and 189, 190, 125. Subantarctic species also extend, in small numbers, through Stations 218, 4, 198, 208, to 178, 138, and 130. The stations of these three aggregations will be referred to subsequently when it will be found that they were situated in mixing waters (see Figs. 3, 10).

Northern Subantarctic Group

The species selected for the Northern Subantarctic Group were confined to that warmer water (i.e., 11°C. and higher) which is believed to have originated in the higher latitudes of the subantarctic. None was present in the colder waters at Stations 795, 826, or 921 (Fig. 2). Three species have been selected, namely, *Sagitta serratodentata* Krohn var. *tasmanica* J. M. Thomson, *Paracalanus parvus* (Claus), and *Euphausia lucens* Hansen.

Sagitta serratodentata has been described as "cold tolerant," while the variety *tasmanica* is reported to inhabit waters of 11° to 17°C. (Thomson, 1947). John (1936) describes *E. lucens* as predominantly a northern subantarctic species occurring most frequently between 12° and 14°C., which confirms Tattersall's

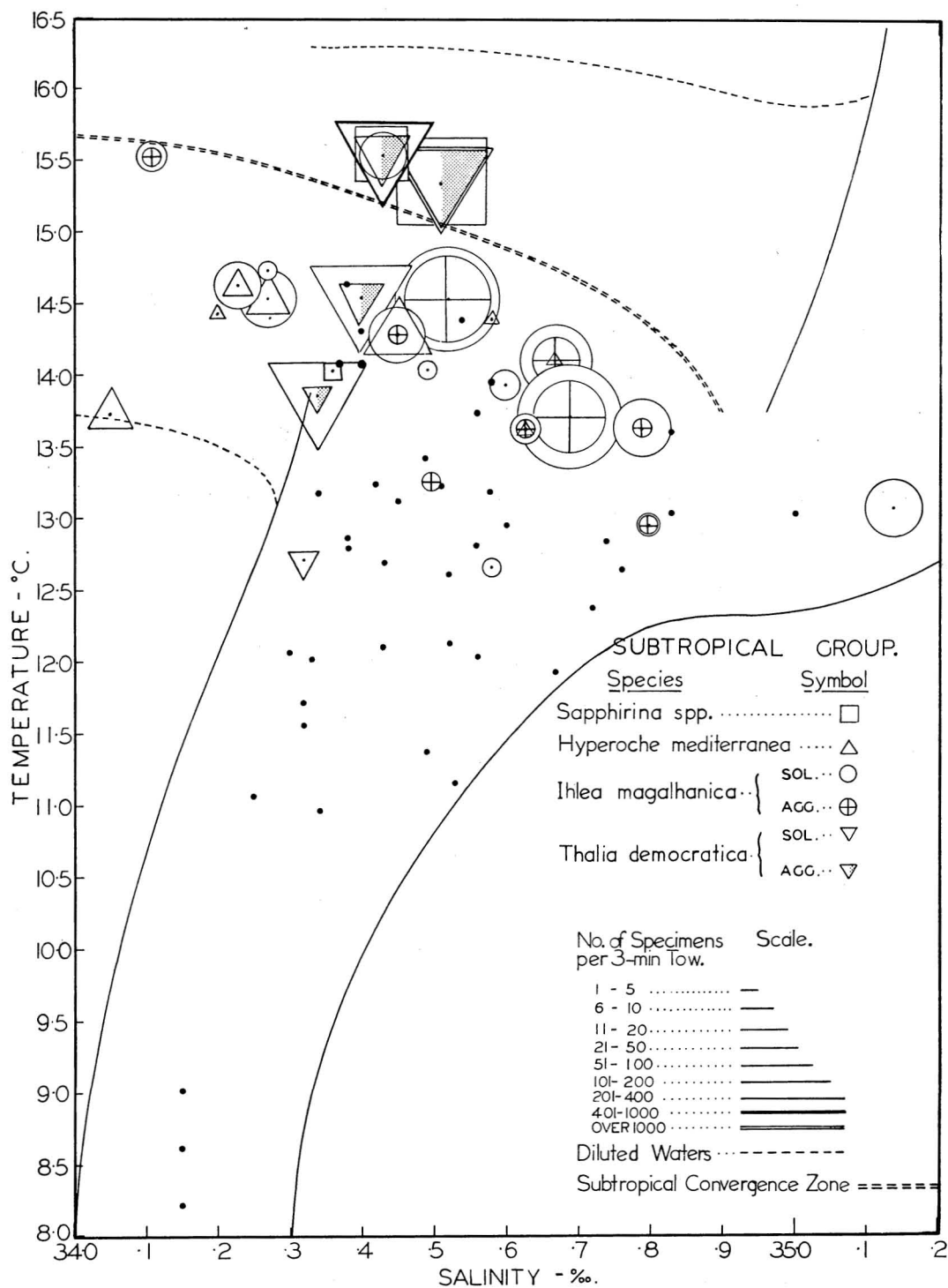


FIG. 8. The distribution of Subtropical species in the T-S-P diagram. Species are almost confined in the warmest water. Plankton stations at which no specimens of the group were taken are shown by ●

(1924) appreciation of its distribution. Thus the distribution of these species as shown in the T-S-P diagram (Fig. 7) agrees with previous accounts. The distribution of *P. parvus* is restricted to that recorded previously (see p. 17).

The distributions of the species and the numbers captured relative to temperatures and salinities are shown in Figure 7. It is evident that the numbers taken were often large. All species were strongly represented at Stations 292, 330, 310, 79, etc., and 189, 190, (referred to as being in mixed waters in the discussion of the Southern Subantarctic Group), but are present only as rarities, or are absent from collections at other stations in coastal-subtropical waters. Reduced numbers were taken at Stations 212 and 214 in colder waters. As these were night stations this reduction may be a reflection of the effects of the lower temperatures. At some other stations in these colder waters, e.g., Stations 5, 191, 6, specimens were absent or rare, but this may be a result of the stations being occupied in daylight.

Not only do the Northern Subantarctic species inhabit the comparatively warmer water of subantarctic origin, but they can penetrate into warm mixed waters in larger numbers than any of the Southern Group of species. This may be consequent on their adaptation to higher temperatures in their more usual habitat. According to John (1936), there is a gradual amelioration of conditions, with changes in the composition of the planktonic fauna to correspond, as one proceeds from colder to warmer northern waters in the subantarctic. Therefore the abrupt transition suggested by the convenient subdivision of the species into Northern and Southern Subantarctic Groups probably over simplifies the faunal distribution. Further sampling at temperatures lower than 11°C. may demonstrate a gradual decrease in the frequency of occurrences and in the number of species taken of the Northern Subantarctic Group—a decrease which would accord with John's views. How-

ever, such would not necessarily detract from either the Southern or Northern groups of species as indicators of the particular conditions for which they have been selected.

Subtropical Group

The species of the Subtropical Group have been selected on the basis of their previous distributional records. Although detailed sampling is required in those New Zealand waters which are beyond doubt of subtropical origin in order to demonstrate that the species originated there, it is believed that they are typically of the subtropical population. The species selected are *Sapphirina* sp., *S. angusta* Dana, *S. gemma* Dana, *S. sali* Farran, and *S. pyrosomatis* Giesbrecht (see Wilson, 1932), *Iblea magalhanica* Apstein, *Thalia democratica* Forskal (see Thompson, 1942, 1948), and *Hyperoche mediterranea* Senna (Stephensen, 1924, Hurley, 1955). Of these, *H. mediterranea* did not occur at Stations 322 and 326, and *Sapphirina* spp. were taken only at these stations.

The wide range of salinities (Fig. 8) over which these species are taken points to their tolerance in this regard. On the other hand, the species maintain a close association with the warmest water and only exceptionally are specimens taken outside of it. The group thus strongly contrasts with the two Subantarctic groups.

The species of this group are normally associated with subtropical water. In this survey they occur largely in the warmest water (Fig. 8), and therefore it is suggested that this water is of, or is being influenced by, water of subtropical origin. Except for Stations 322 and 326, the majority of the collections of the Subtropical species were from stations of Series 1 (see Figs. 1, 3), mostly within Foveaux Strait, i.e., within the area expected to be most strongly influenced by any eastward flow of water from subtropical sources. The few other occurrences of the species usually are associated with coastwise extensions of the subtropical influence.

It may be coincidental that the Subtropical species have proved adequate to indicate the waters of subtropical origin from both east and west of New Zealand. If further investigation shows that the faunas are dissimilar, separate indicator groups would probably need to be established for the waters of each of these areas.

Coastal Group

Species indigenous to coastal waters must necessarily be tolerant of the considerable fluctuations in temperature and salinity which may occur in these waters. The species of the Coastal Group are distinguished from the Subtropical Group by occurring over a much wider range of temperatures (Figs. 8, 9). Six species have been selected, namely *Tenagomysis macropsis* Tattersall, *T. tenuipes* Tattersall, *Parathemisto* (*Euthemisto*) *gracilipes* Norman, *P. (E.) australis* Stebbing, *Nyctiphanes australis* Sars, and *Oikopleura dioica* Fol. *Nyctiphanes australis* is a recognised coastal species (Sheard, 1953), as is *O. dioica* (Thompson, 1948). *Tenagomysis* spp. have been confined almost completely to neritic conditions (Tattersall, 1918, 1923; Bary, 1956). *Parathemisto australis* has been collected previously only in coastal areas (Stebbing, 1888; Barnard, 1930), which is true of the present material (Hurley, 1955). *Parathemisto gracilipes* occurred in similar localities to, and was often captured with, *P. australis*, although the literature describes it as an oceanic species. Of these species only one specimen of *N. australis* was captured in water of unquestioned subantarctic origin (Station 212, Fig. 9), presumably as a stray. On the other hand, all species were present very commonly at stations where subantarctic water is believed to have been mixing with coastal water (Stations 292, 310, 330, etc., and Stations 189, 190, 125). A few specimens of *Parathemisto* spp. were taken at Station 322—suggestive of coastal water at the station. The occurrences of Coastal species at Stations 124 and 128 are not incon-

sistent. These stations lie in highly saline water which appears to be originating in a large shallow inlet on the north coast of Stewart Island (Patterson Inlet, Figs. 1, 12), and it is this water which locates the stations in the part of the diagram representing subtropical water (Fig. 3).

There is a general, but patchy, distribution of Coastal species throughout the coastal water, from high to low salinities and up to the highest temperatures. Nevertheless, they are almost completely absent from subantarctic water, even when it is contiguous with coastal water. It is believed that the species either are unable to survive being transferred from the coastal into subantarctic water, or that some physical process at the boundary between the waters prevents such a transfer (see pp. 48–49).

INTERRELATIONSHIPS BETWEEN SPECIES' GROUPS, AND TEMPERATURES AND SALINITIES

The interrelationships of the species' groups and their correlation with temperatures and salinities are shown in Figure 10. The groups are distinguished in the figure by hatching, and a subjective estimate of the abundance of each is indicated. The "area of chief concentration" is demarcated by lining-in and represents that portion of the diagram in which the bulk of each of the groups was captured.

As particular organisms are undoubtedly characteristic of particular waters, those instances where species from several waters are found together are believed to represent areas of mixing waters. Figure 10 illustrates that there are aggregations of stations (already referred to) from which large mixed catches were consistently made. Stations 292, 330, 310, 279, 304, 40, and 79 (refer also to Fig. 3) form one aggregation and Stations 189, 190, and 125 another. All four species' groups were present at most stations of the first aggregate, which indicates that the collections are from a mixture of the three waters. Subtropical species were absent from stations of the second

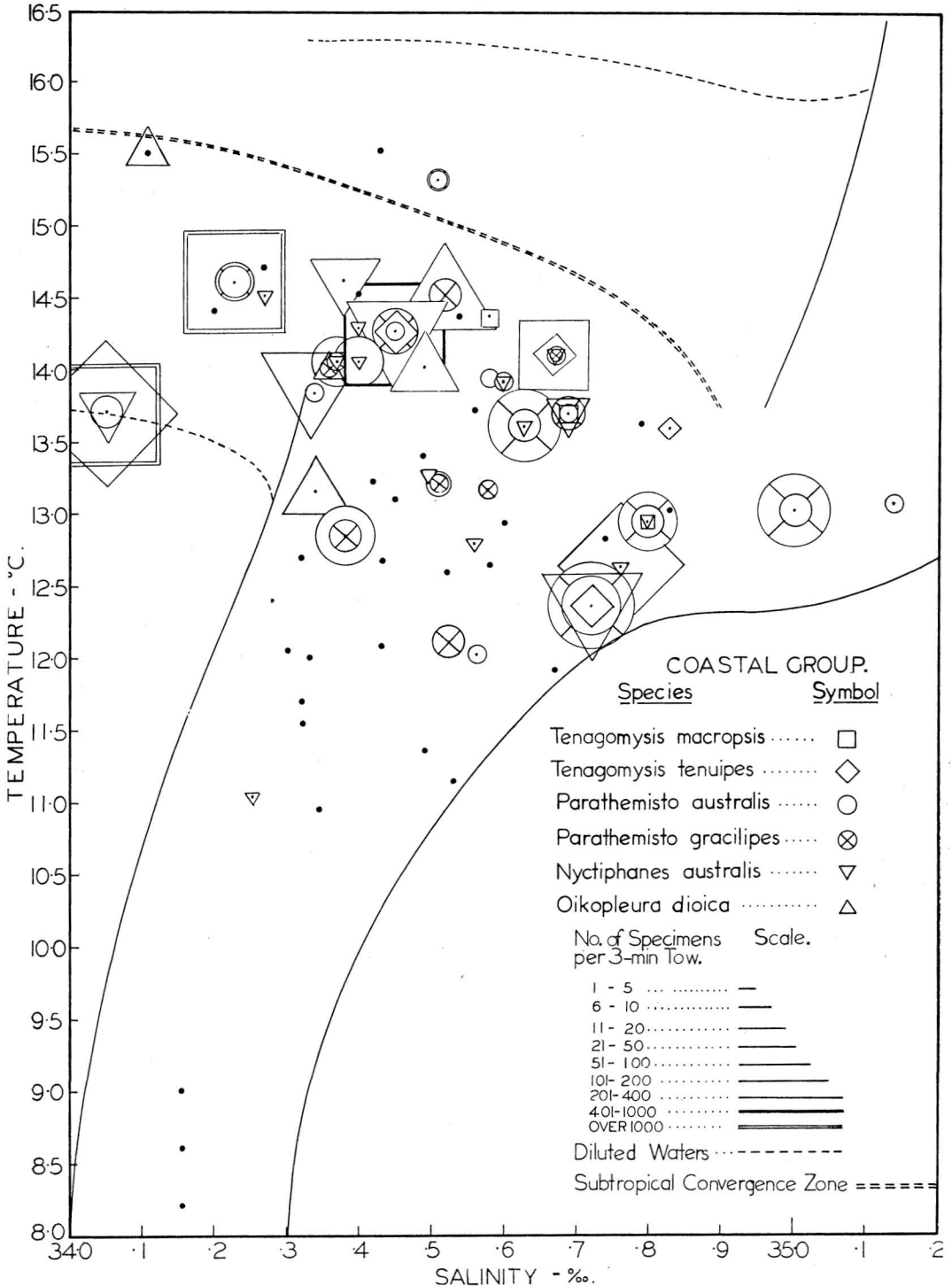


FIG. 9. The distribution of Coastal species in the T-S-P diagram. These species occur commonly over comparatively wide salinity and temperature ranges. They do not occur in subantarctic water except where it is intruding into, and mixing with, the coastal water. Plankton stations at which no specimens of the group were taken are shown by ●

aggregation (except Station 125), suggesting little or no influence from water of subtropical origin. A third group of stations yielded comparatively small mixed catches of Coastal, Subtropical, and "Tolerant" Southern Subantarctic species, which indicates that mixing was also taking place. This mixing may have been on a minor scale or the small catches may be due to the tows being made in daylight. The stations form a discontinuous series extending more or less vertically through the diagram to terminate at Stations 130 and 138.

The distributions of the groups in Figure 10 are brought about by movements of the waters of which they are indicators. Therefore, the general courses of such movements should be traceable from these distributions. The fact that subtropical oceanic species are present in the coastal water indicates that water of subtropical origin is moving into the coastal water. Similarly the distribution of the Subantarctic species shows they also are being carried into the coastal water. These movements are shown by stippled arrows in Figure 10. Those portions of the T-S-P diagram which are illustrative of intensive mixing of plankton and waters suggest that, as well as these general movements, there are others in which there is a more vigorous, localised penetration shorewards. It would seem that these are predominantly of water of subantarctic origin, intruding into coastal water.

A number of the stations of each of the regions of mixed waters in Figure 10 are widely distributed geographically and in time. Nevertheless, where similar environmental properties have ensued on the mixing of the waters, the group composition of the plankton hauls, and often the quantity collected, are comparable. Thus in this T-S-P diagram, the selected representatives of the zooplankton emphasise and enable the identification of those stations at which mixing of waters is inducing similarities in the environmental conditions. Conversely, the diagram shows for those stations at which one group of spe-

cies is present, or predominates, that the water is entirely or predominantly of that mass for which the species constitute an indicator group.

It can be argued with respect to the "faunal island" about Stations 322 and 326 (Fig. 10) that more frequent sampling would have revealed a continuity in the species distribution between these and other stations of the series (Fig. 2). In all, seven salinity-temperature and plankton stations were occupied near to and north of what is believed to be the subtropical convergence (Figs. 4*a*, 19*b*), and all are located in the T-S diagram (Fig. 3) in water of subtropical origin.

Waters of mixed properties undoubtedly occur about the convergence. However, should water of either subtropical or subantarctic origin be present in slightly greater quantity, stations would tend to aggregate in the one or the other in the T-S diagram. The predominating water would be reflected in the species which were present. On the other hand, if samples are from truly intermediate conditions, an intermediate position would be occupied in the diagrams; but if the transition zone is narrow (as in the present traverse, see Fig. 4*a*), such samples would be rare. The subtropical group of species predominated at Stations 322 and 326, which agrees with the stations being north of the convergence and in water largely of subtropical origin (some Subantarctic species were taken, but they are believed to have originated in the subsurface subantarctic water, see p. 47). In the circumstances, therefore, it seems reasonable to separate Stations 322 and 326 from the remainder.

GEOGRAPHICAL DISTRIBUTIONS OF TEMPERATURES, SALINITIES, AND SELECTED SPECIES, AND CORRELATION OF THESE WITH THEIR DISTRIBUTIONS IN T-S-P DIAGRAMS

A sequence of geographical charts incorporating synoptic or quasi-synoptic collections of temperatures and salinities should demonstrate cyclical or other changes in the distri-

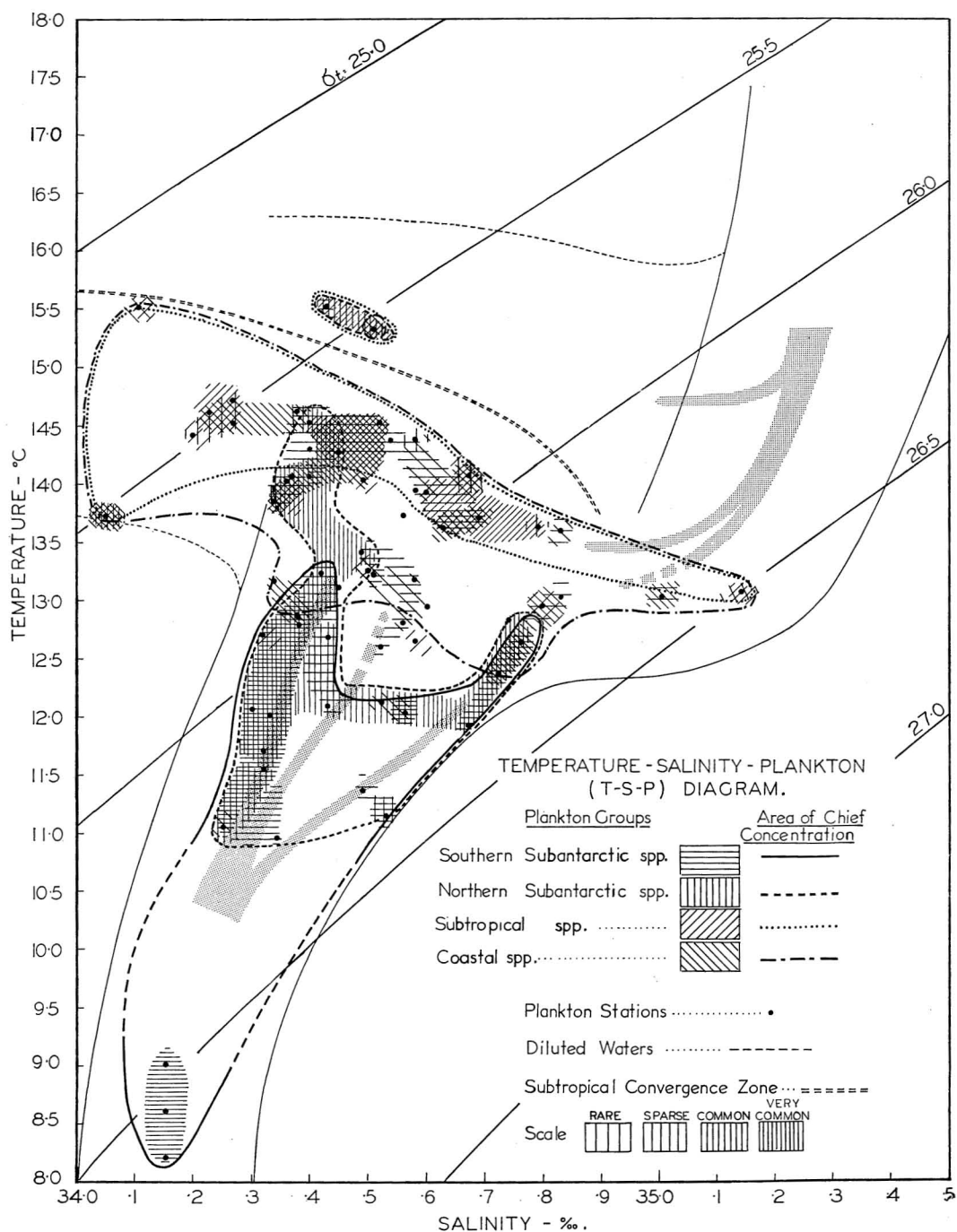
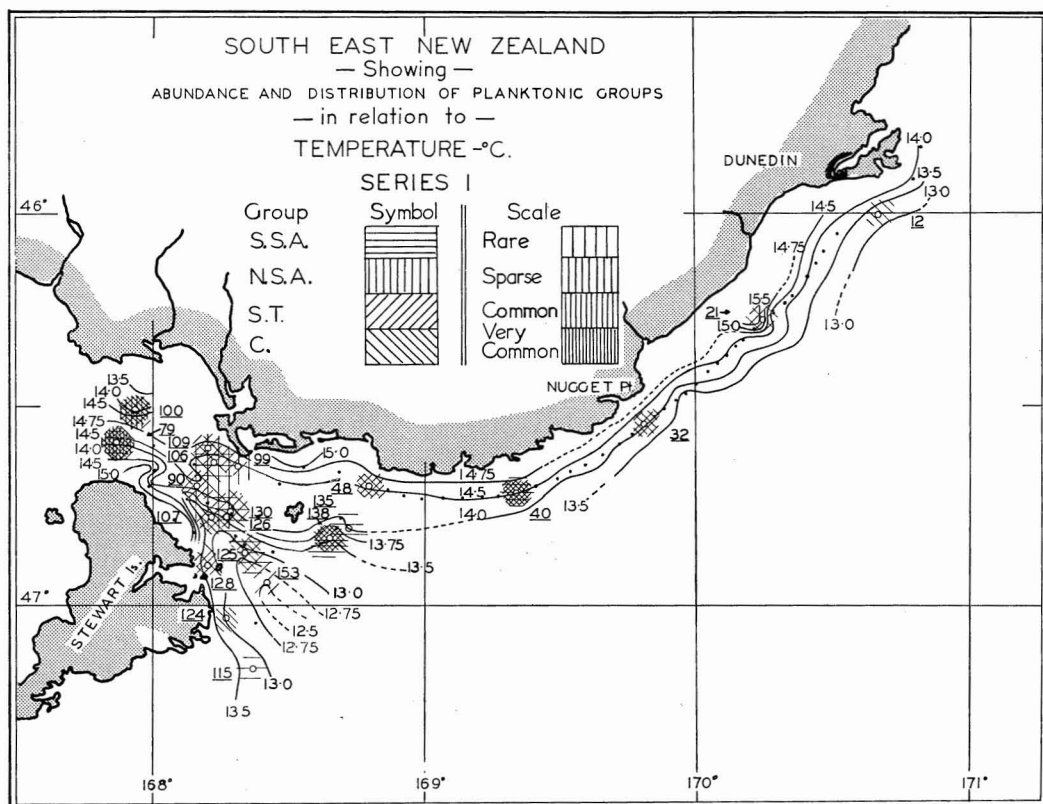


FIG. 10. A generalised T-S-P diagram in which the distributions and interrelationships of the four planktonic groups from the waters about southern New Zealand are shown. Note the three areas where mixed plankton catches indicate that mixing of waters is taking place. The water envelope is as in Figure 3; only plankton stations are entered.



FIGS. 11, 12. Series 1, Stations 10-153, January 6-24, 1951. The distribution of Southern and Northern Subantarctic, Subtropical, and Coastal species in relation to Figure 11, Temperature, °C.; and Figure 12, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperatures or salinities additional to those taken at plankton stations •; plankton station numbers are underlined.

butions of the properties of an area. In turn such changes may be correlated with variations in the geographic distribution of the plankton to yield information showing the causes and effects of water movements on species distribution. Accordingly the geographical distributions of water properties and of plankton groups are discussed for the stations of Series 1 to 7. The relationships thus disclosed are considered with reference to the distributions in the T-S-P diagrams.

Series 1. Stations 10 to 153; 6 to 24.I.51

The stations of Series 1 were accumulated over a period of 18 days. Of these, Stations

10 to 48 were occupied during January 5 to 6, 1951. Charts of the distributions of temperatures and salinities (Figs. 11, 12) illustrate an average of conditions because of the length of time involved.

Warm, comparatively highly saline water extends from the western and central Straits along the South Island coast, and has probably originated in that Tasman Sea water which has been deflected to the southward along the west coast of South Island. It is being diluted by fresh water. Other highly saline water appears to be entering from Patterson Inlet, and spreads thence south-eastwards along the coast of the island. Cooler water (Fig. 11) is present as a tongue-like intrusion

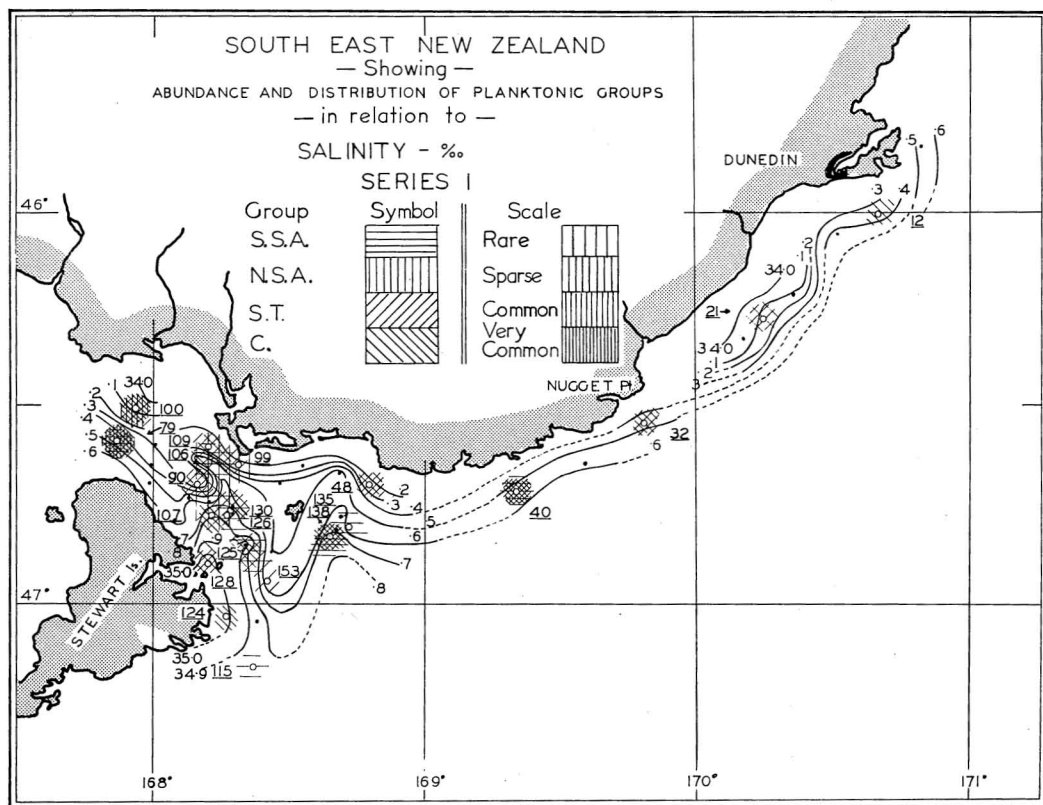


FIG. 12. See legend for Figure 11.

from the southeast. However, the distribution of salinities suggests that highly saline water has spread throughout the area.

Only some general features of the plankton distribution in relation to that of the water properties will be discussed. From the T-S diagram (Fig. 3) it is apparent that the stations of Series 1 lie predominantly in the warmest waters, only a few being slightly influenced by the cool water from the southeast—a condition conforming more to that indicated by the distribution of salinities (Fig. 12). However, the T-S-P diagrams (e.g., Figs. 6, 10) demonstrate that Subantarctic species were present, in small numbers, at several of the stations. Thus indications are that water of subantarctic origin is entering Foveaux Strait, some of it probably from the southeast, as is suggested by the conformation of the isotherms (Fig. 11).

Station 79, and the geographically close Station 100, both possess a strong representation of Subantarctic species. In the T-S-P diagram (Fig. 10) Station 79 forms one of that group of stations at which occurrences of all plankton groups are suggestive of a mixture of all waters. It is likely, therefore, that subantarctic water is present, entering probably from the west, along with mixed coastal-subtropical waters. That the influence of this subantarctic water is weak is suggested by both the positions of Stations 79 and 100 in the T-S diagram (Fig. 3), and the lack of any indication of the water about them in the relevant geographic charts (Figs. 11, 12). Station 138 is in that part of the T-S-P diagram (Fig. 10) representative of mixing on a minor scale, and Subantarctic, Coastal, and Subtropical species were collected. The configurations of the isolines indicate a small-

scale intrusion of water of subantarctic origin into coastal-subtropical waters at Station 138. Thus the planktonic occurrences accord with the influences bearing at that point.

Occurrences of zooplankton at other stations could be individually discussed, and rational explanations of the presence or absence of groups can be advanced for many of them, but the detailed picture that results is a confused one. The waters are very mixed. The distributions of the species' groups are to an extent reflecting this state, which is aggravated by the long period over which sampling continued.

It is reasonable to deduce, from the physical data presented in Figures 11 and 12, that there is some influence from water of subtropical origin in Foveaux Strait. The presence of typically Subtropical species is supporting evidence. More conclusive evidence for the influence is demonstrated, however, from the distributions of the Subtropical species in the T-S-P diagrams (Figs. 8, 10, in particular). The occurrences of these species coincide with the distribution of the warmest waters which are in such a position as to be contributed to directly from the subtropical mass (Figs. 3, 10). Subtropical species were collected also at stations in later series (Stations 178, 199, 239, 292, 304); these occurrences are indicative of coastwise extension of the subtropical influence.

Series 2, Stations 159 to 192; 29.I.51 to 1.II.51

The stations of Series 2 (excepting along the coast of South Island) are eastward of, and a little further to seaward than, those in Series 1 (Figs. 1, 13). Cooler temperatures than those in Series 1 prevail along the coast of South Island, and there is a broad intrusion of cool water (Fig. 13) from the south and east. There is, too, an admixture of high salinity water throughout the sampled area (Fig. 14). A northwest to southeast displacement of the isolines about Stations 189 and 190, eastward of Steward Island, suggests that

warm, high salinity water is present, possibly from Foveaux Strait.

Very common occurrences of Northern and Southern Subantarctic groups of species at Stations 187, 188, 189, 190, and 192 are believed to be indicative of a strong influence from water of subantarctic origin (Figs. 7, 10). Common occurrences of Coastal species at Stations 189 and 190 point as well to mixing between the coastal and subantarctic waters about these stations, and also suggest that the high salinity water extending from Patterson Inlet does in fact originate there, and is not an intrusion from other oceanic sources. The occurrences of the planktonic groups in relation to the geographic distributions of water properties (Figs. 13, 14) provide a similar picture. Stations 189 and 190 lie on the southwest side of the intruding low-temperature water. Mixing is undoubtedly taking place about these stations between this and the warm, saline Straits water. The collections of mixed planktonic groups confirm this. Stations 187, 188, 191, and 192 are closely associated with the intruding cool water (Fig. 13), which the predominance of Subantarctic species indicates is of subantarctic origin.

Stations 178 and 165 lie in high salinity, warm inshore water (Figs. 13, 14), and the Coastal and Subtropical species at both stations are in agreement with this. In addition, mixing with subantarctic water is indicated for Station 178 by the Subantarctic species occurring there. The regularity of the isolines in the vicinity of the station denotes that the waters are mixed, which agrees with Station 178 being (together with Stations 138, 135, and 130, Series 1) in that portion of the T-S-P diagram (Fig. 10) representing mixing of waters on a minor scale.

Stations 187 to 192 are moderately separated geographically, but their grouping in the T-S-P diagram demonstrates a certain homogeneity of environmental conditions. The diagram heightens the effect that coastal water has on the composition of the plankton

at Stations 189 and 190, but at the same time demonstrates an overall influence from Subantarctic species which are being introduced by water of subantarctic origin.

Subantarctic species, and water of subantarctic origin, are more in evidence at stations of Series 2 than at those of Series 1 (for which Subtropical species indicate that at least some of the water has originated in the subtropical mass). The differences between the series are concisely illustrated by the T-S-P diagrams (Figs. 7, 8, 10).

Series 3. Stations 193 to 228; 5 to 13.II.51

The beginning of Series 3 is separated by four days from the end of Series 2. In Series 2, lower temperatures than in Series 1 pointed to an increased subantarctic influence off the coast of South Island. In Series 3, cool, low-salinity water has intruded strongly towards the coast, centred a little to the west of Stations 216 and 218 (Figs. 15, 16). This intrusion appears to be acting as a barrier to an east-going coastwise movement of warm, high-salinity water, causing it to spread in a fanlike manner towards the southeast. High salinities and temperatures to the east of Stewart Island suggest that some of this water may be escaping in a narrow zone along the coast of the island. The isohalines and, to a lesser extent, the isotherms indicate that the influence of the cool, low-salinity water extends well in towards the Strait.

Apart from an exceptional occurrence of a Coastal species at Station 212, the plankton taken at Stations 210, 212, 214, 216, 218, and 206 is entirely of Southern and Northern Subantarctic groups (Figs. 10, 5, 6, 7). The water at these stations, therefore, is regarded as being of subantarctic origin. The stations are moderately separated geographically (Figs. 1, 15). However, their aggregation in the T-S and T-S-P diagrams (Figs. 3, 10) emphasises an essential homogeneity of the water which the occurrences of the subantarctic species confirm.

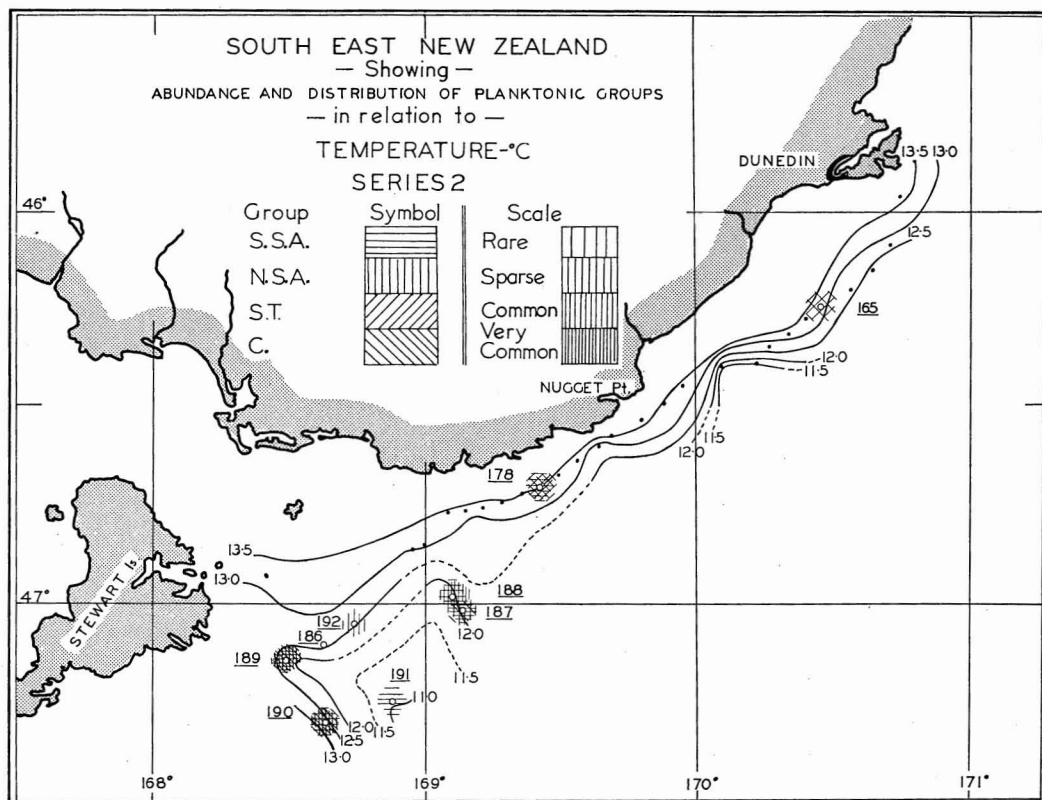
Four stations, namely 218, 208, 198, and 199 are located in water of slightly higher salinity (Fig. 10) than the other stations of the Series, possibly as the result of coastal water mixing with that from the subantarctic. Occurrences of Coastal plankton at 208 and 198 support this view; the subantarctic influence is evident from the Southern Subantarctic species captured at 218 and 198, and Northern and Southern Subantarctic species at 208. (No selected species were taken at Station 199.) From the geographic charts Station 218 appears from its temperature (Fig. 15) to be influenced by subantarctic water; on the other hand, the comparatively high salinity suggests some influence from coastal-subtropical water. As Southern Subantarctic species only were taken, the latter influence was not confirmed by the plankton haul. The temperature and salinity at Station 208 indicate that it is located in mixed waters and its plankton content supports this.

It is of interest that the distribution of the selected Subantarctic species of Series 3 indicates that uncontaminated water of subantarctic origin has a restricted salinity range of between about 34.2 and 34.45 ‰ (Figs. 3, 10).

There are distinctive characteristics to the species composition of stations in this, as compared with the previous two series, which are readily seen from the T-S-P diagrams. They are believed to be directly attributable to the different properties which are evident between the waters of the three series. Unlike Series 1 and 2, water of subantarctic origin is dominant in Series 3, and the occurrences of the Subantarctic species coincide with and, in fact, delineate its extent in the diagrams (Figs. 5, 6, 7, 10).

Series 4. Stations 229 to 314; 8 to 9.III.51

The collections of this, and the subsequent, series are as nearly synoptic as is possible from a single ship. Stations of Series 4 were occupied approximately one month later than those of Series 3.



FIGS. 13, 14. Series 2, Stations 159-192, January 29-February 1, 1951. The distribution of the four planktonic groups in relation to Figure 13, Temperature, °C.; and Figure 14, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperatures or salinities additional to those taken at plankton stations •; plankton station numbers are underlined.

When compared with Series 3, higher temperatures near the coast of South Island (Fig. 17) point to a restoration of the influence of mixed coastal-subtropical waters, originating probably in the west. A slight influence from water of subantarctic origin is indicated by the shoreward deflections of isotherms south of Nugget Point. The pronounced shoreward bulges of isotherms and isohalines at a number of other localities are suggestive of stronger influences from the same source (Figs. 17, 18). The conformation of these isolines may suggest as well an offshore movement of coastal water in adjacent areas. Steep temperature gradients between the warm saline coastal and the cool, less saline

oceanic waters are suggestive of mixing, over short distances. There is an area of more general mixing extending from shortly south, to north, of Dunedin.

In the T-S diagram (Fig. 3) the plankton stations of Series 4 lie in a group between 11.75° and 14.5°C., and (all but Station 239), between 34.3 and 34.4 ‰ salinity. Thus they are closely associated with Stations 212, 214, etc., of Series 3. At each of Stations 270, 285, 297, 301, and 308 there is a strong representation of Northern and Southern Subantarctic planktonic groups (Fig. 10). Therefore, the position of the stations in the T-S diagram, and their plankton content, associate them with the water of subantarctic origin. The

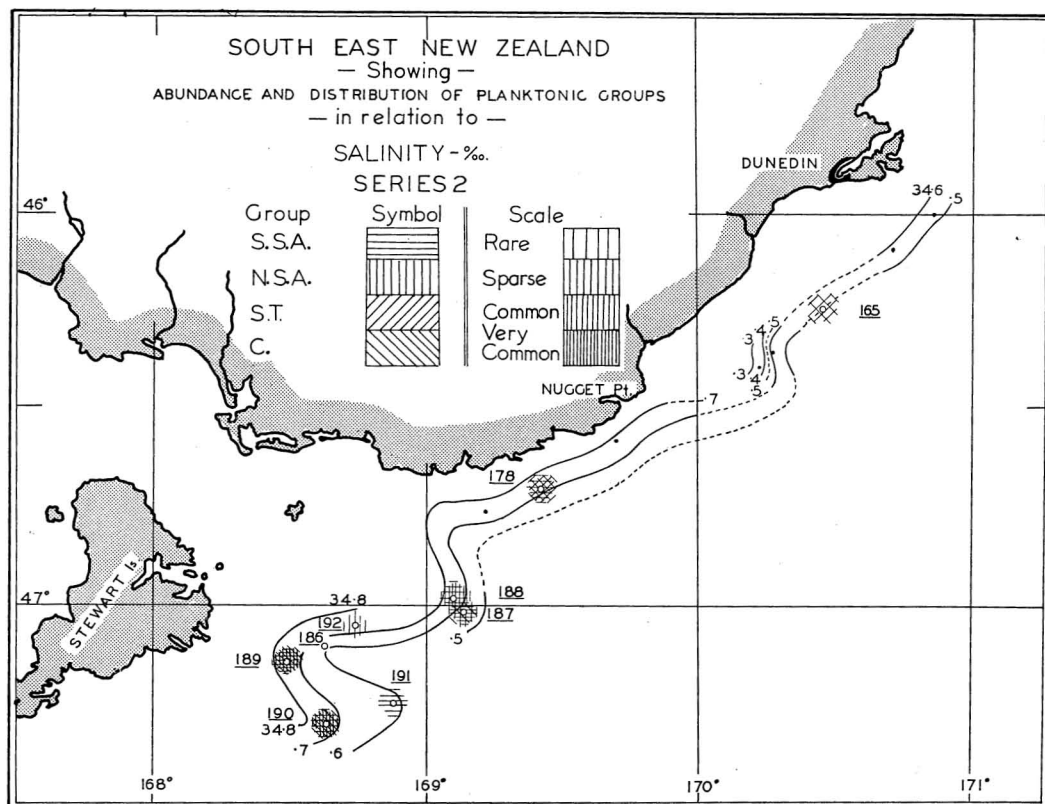


FIG. 14. See legend for Figure 13.

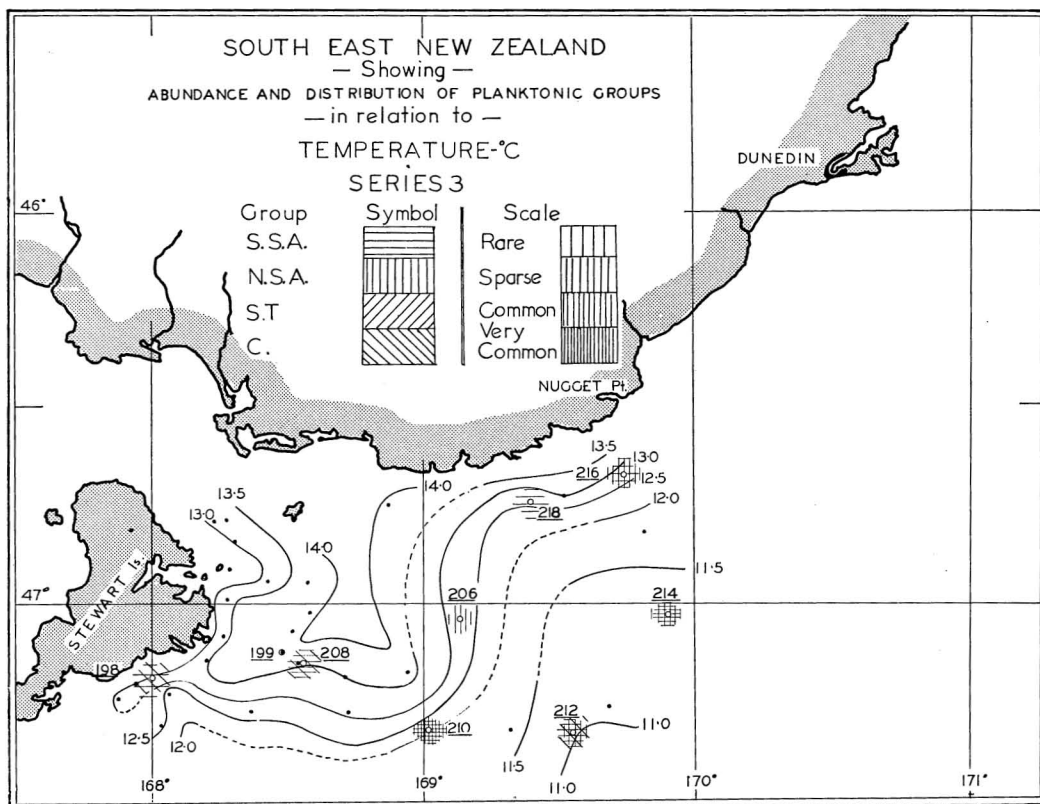
subantarctic influence is confirmed by the geographical distribution of temperatures at Stations 285 and 297 (Fig. 17), and salinities at 270, 301, and 308 (Fig. 18).

Of the remaining stations in Series 4 (Stations 292, 310, 279, 244, 304, and 239), Station 239 lies in coastal water (Fig. 10), but exceptionally contained a rare representation of the Southern Subantarctic Group; this group was present also at Station 244. Temperatures indicate that subantarctic water may be influencing these two stations (Fig. 17) which possibly explains the plankton occurrences. Nevertheless Coastal and Subtropical planktonic groups would have been more appropriate, especially at Station 239.

Stations 292, 310, 279, 304, and 244 are grouped together in the T-S-P diagram and

the mixed Coastal, Subtropical, and Subantarctic (mostly Northern) plankton at most of them denotes they are sampling in a mixture of subantarctic and coastal-subtropical waters. Isotherm configuration (Fig. 17) indicates that, following an initial mixing between water of subantarctic origin (as is present at Stations 285, 297, and 308) and coastal water, the influence of the subantarctic water continues shorewards towards Stations 279, 292, and, to a lesser degree, 310. Isohalines (Fig. 18) point to Station 304 being influenced by water of subantarctic origin as well.

Series 4 is important for two reasons. First, Stations 292, 310, 279, 304, and 244 form a compact group in the T-S-P diagram (Fig. 10). These are geographically isolated sta-



FIGS. 15, 16. Series 3, Stations 193-228, February 5-13, 1951. The distribution of the four planktonic groups in relation to Figure 15, Temperature, °C.; and Figure 16, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperature, salinity additional to those taken at plankton stations •; plankton station numbers are underlined.

tions, but they are aggregated because of similarities of hydrological and biological properties, which are the result of invasions into coastal water, at several localities, of water of subantarctic origin. Second, coastal and subantarctic waters in the T-S and T-S-P diagrams are linked through a continuous series of stations. Such a linkage demonstrates beyond reasonable doubt that the Subantarctic plankton collected in the coastal area originates, and is transported, in water of subantarctic origin which is penetrating shorewards (and at the same time is being warmed). These two facts thus contribute evidence in support of an earlier statement that planktonic content of mixing waters may be utilised to indicate the sources of the waters being

mixed.

The T-S-P diagram (Fig. 10) emphasises the similarities in planktonic content and hydrologic conditions between Series 3 and 4, even though they are separated geographically by at least 60 miles, and by almost a month in time. Of interest also, is that while subantarctic groups penetrated into warmer waters at Stations 279, 292, 304, and 310, coastal species did not penetrate to Stations 285 and 297, lying predominantly in subantarctic water. Coastal and Subtropical species rarely were taken in subantarctic water, even when, as at these stations, the collections were made at the extremities of what may be regarded as offshore directed movements of coastal water.

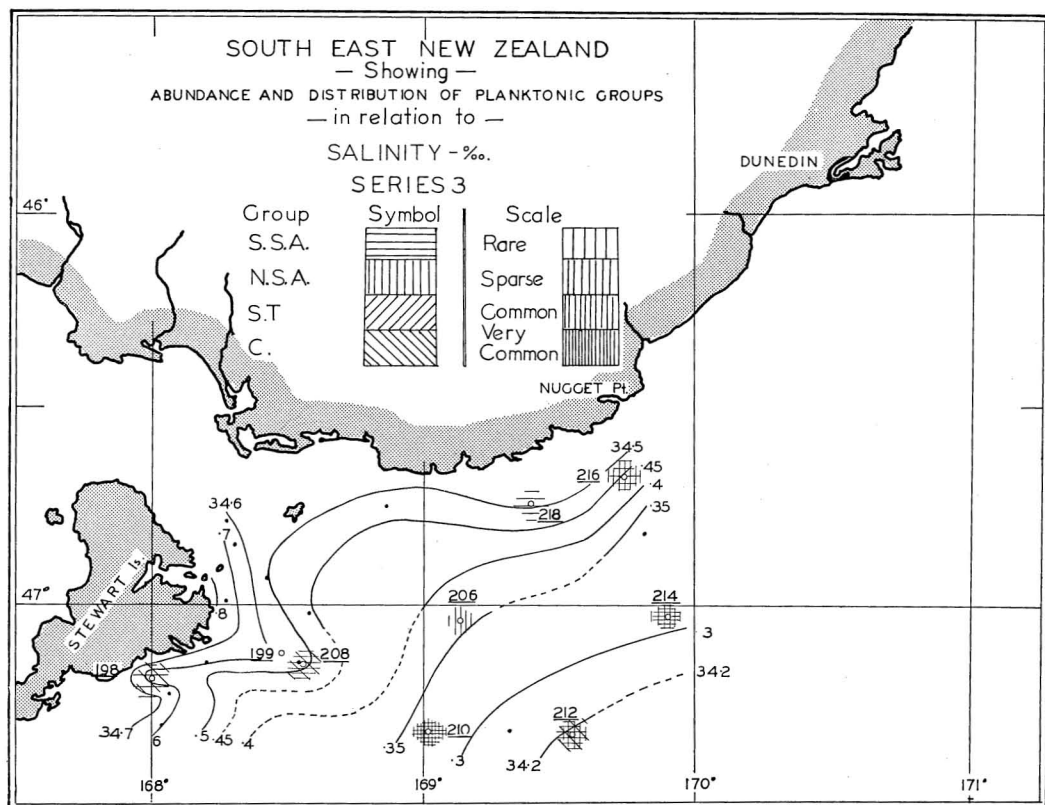


FIG. 16. See legend for Figure 15.

Series 5. Stations 1 to 6; 3 to 4.I.51

Stations of Series 5 and 6 were occupied during cruises between Wellington and Dunedin in January and March, respectively. Stations of Series 5 precede those of Series 1 by three days, but their discussion has been deferred for convenience of comparison with those of Series 6.

The stations of Series 5 are believed to sample either from water of subantarctic origin, or from a mixture of this and high-salinity, but *cool*, coastal water. The temperature and salinity at Station 5 (Figs. 19a, 20a) indicate the presence of water of subantarctic origin only. At Station 6 this water is predominant, but the slightly increased salinity points also to coastal water being incorporated. Higher salinities again at Stations 1 to

4, indicate an increased admixture of the coastal water. The steady rise in temperature northwards along the coast probably reflects a latitudinal increase. However, the distributions of temperatures and salinities demonstrate that the water is essentially homogeneous and predominantly of subantarctic origin. Supporting evidence comes from the planktonic occurrences.

Either or both Northern and Southern Subantarctic groups occur at Stations 2 to 6 (none of the species captured at Station 1 was among those selected). Coastal species were present at Stations 4 and 3, but they do not occur elsewhere. These distributions indicate the influence of subantarctic water at all stations, together with that of coastal water at Stations 3 and 4.

In the T-S diagram (Fig. 3) Stations 5, 1,

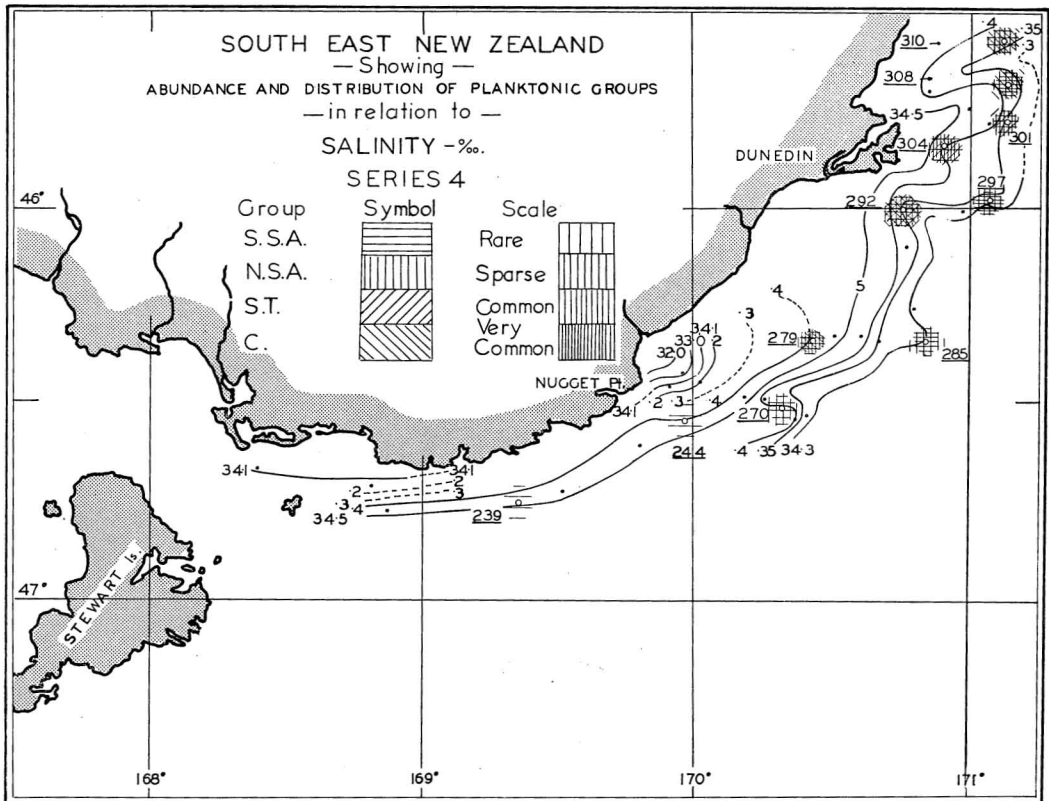


FIG. 18. See legend for Figure 17.

and, incidentally, makes for readier identification (in the T-S-P diagram) of the mixed sample.

Series 6. Stations 320 to 343; 21 to 22.III.51

These stations were occupied in March, and the shoreward extremity of the subtropical convergence now transects the series (see p. 22). Stations 320 to 328 are north of the convergence, 331 to 343 to the south of it; Stations 329 and 330 are near to the meeting zone of the subtropical and subantarctic waters (Figs. 4a, 19b, 20b).

Subantarctic water is strongly evident, through low temperatures and salinities, only at Stations 341 to 343. Northwards towards the convergence there is a pronounced coastal influence shown by high temperatures and

also by increased salinities (salinities decrease farther inshore as a result of dilution with fresh water). North of the convergence, the salinities at some stations approach those of open ocean subtropical water (about 35 ‰), but dilution is apparent and to a considerable degree at Stations 322 and 326.

Southern and Northern Subantarctic species occurred at Station 326, and Northern species at 322. They are probably to be accounted for by upward migration of the organisms from the subsurface subantarctic water.

The occurrences otherwise of the several planktonic groups conform to the distribution of the waters. Station 342 has only Subantarctic groups present, but at Station 337 these groups are rare and the Coastal Group predominates. At Station 330 there is a mix-

ture of the four groups, but at 326 and 322 the Subtropical Group is dominant.

The T-S-P diagram (Fig. 10) illustrates the general correlation between the occurrences of planktonic groups and the distribution of the water properties shown in the geographical charts. Station 342 is the only one clearly in subantarctic water and its fauna is entirely of Subantarctic groups. Station 330 is situated in the portion of the T-S-P diagram representative of water of subantarctic origin intruding into, and mixing with, coastal-subtropical waters. The four planktonic groups are present, which is consistent. However, both its position in the T-S-P diagram, and the predominance of Subantarctic species indicate that the subantarctic influence is strongest. Station 337 lies just outside the larger of the subantarctic intrusions in the T-S-P diagram. Isotherms and isohalines (Figs. 19*b*, 20*b*) suggest a strong coastal influence, which is confirmed by the predominance of Coastal species. Stations 326 and 322 are separated from all other plankton stations by the subtropical convergence. Both occur in water of subtropical origin, somewhat diluted by lower salinity coastal water, and Subtropical species predominated in the plankton.

It is important that the species' occurrences of Series 6 indicate the approximate position of the subtropical convergence. A comparison of faunal distributions, as well as physical data, of Series 5 and 6 show that the convergence has moved southwards during the three months separating the series.

Series 7. Stations 795 to 921; 13 to 17.XI.51

The stations of this series have enabled the source of the Southern Subantarctic species to be demonstrated, and have distinguished them through their origin in cold water from the Northern Subantarctic group. The temperatures and salinities of the stations are within those given for subantarctic water by Deacon (1937). Because water samples were lost, the salinities of the three plankton stations 795, 826, and 921 have been arbitrarily

chosen from within the range indicated by other stations in the series. The north-going component in the West Wind Drift, ensures that the influence of water in the latitudes of Stations 826 and 921 eventually will be felt about southern New Zealand. Through its agency, the more adaptable of Southern Subantarctic species will be transported to the nearshore waters. The temperature at Station 795 was 2°C. lower than any from which the Northern Subantarctic Group was taken. It would appear that this difference may be adequate as a barrier to these species in view of the geographical proximity of the station to Foveaux Strait (Fig. 2).

DISCUSSION

The selection of those species which are most representative of the faunas of particular waters can be made from the species' distributions in relation to temperature and salinity with the aid of the T-S-P diagrams. In turn, the extent of the influence of water bodies entering an area can be assessed through the distribution of the species in the T-S-P diagram, as well as by the temperatures and salinities of the waters. Species selected as representative of the fauna of one water may occur in other waters, often at groups of stations for which there are similar properties of temperature and salinity. The stations of such a group may be widely scattered in time and place, but affinity between them is demonstrable by means of their species' content. Thus the species relate the waters at the stations to their sources, and at the same time demonstrate the direction and extent of the water movements which have brought about the planktonic distribution. Because the species of a group indicate the presence (and source) of a water body, therefore the distribution of this water in another with which it is mixing can be traced in the T-S-P diagram through the distribution of these species.

The study raises problems relating to the transfer of organisms between one body of water (or range of conditions) and another.

Physiological adaptability probably plays a major part in deciding whether a species will survive such a transfer. For example, "Intolerant" species, because they were appar-

ently unable to adapt readily, show sharp reductions in numbers as coastal water is reached, while the more adaptable "Tolerant" species penetrated into it more freely (Figs.

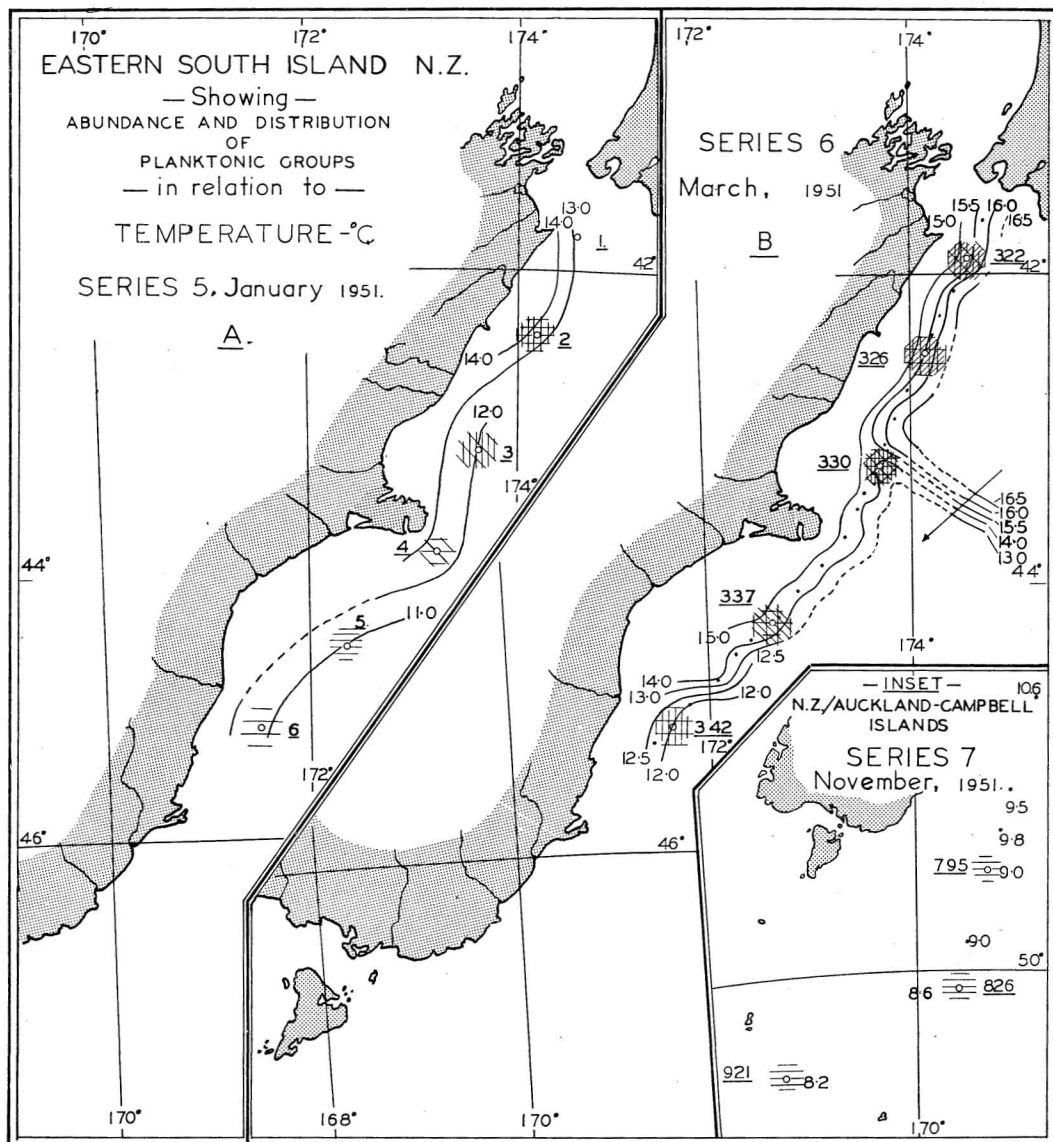


FIG. 19A, B. The distribution of the four planktonic groups in relation to temperature for A. January 1951; Stations 1-6. B. March 1951; Stations 320-343.

INSET: November 1951; Stations 795-921.

The break in temperatures across the subtropical convergence in B are drawn in conjunction with data from the surface thermograph trace, Figure 4b. The symbols for the planktonic groups, and the scale of abundance, are as in Figures 10-21.

5, 6). On the other hand, it has been remarked that Coastal species have not penetrated into water of subantarctic origin. A possible explanation of these facts is that some cold-adapted Subantarctic species can survive the increase in temperatures between cold subantarctic and warm coastal waters, but that coastal species are unable to adapt to lower temperatures. It is difficult to see that this explanation is totally adequate. A preponderant one-way movement of Subantarctic species into coastal areas is demonstrated in the T-S-P diagram (Fig. 10), and is also apparent from analysis of the plankton catches at stations of Series 4 for example (Figs. 17, 18). When oceanic waters move into coastal water, compensatory movements out of the area should ensue. At least some of the low-density inshore water might escape by overriding denser subantarctic water, in which case coastal species would be carried offshore and their numbers gradually decrease as environmental conditions become adversely modified. The opposite appears to be true in most instances. The numbers of the Coastal group of species captured decrease abruptly between 12.5 and 13.0°C. (Fig. 9), as the oceanic water is reached, e.g., as at Stations 285, 297, Series 4. It seems unreasonable to suppose that the abruptly effected absence of the Coastal species results from a sudden application of some physiological factor, and it is suggested that there may be reasons involving hydrological phenomena.

It is possible that the northeast moving current along the coast sets up a superficial transverse circulation (Sverdrup *et al.*, 1942: 676-677) which passes surface oceanic water shorewards. It is conceivable that offshore, surface transport of organisms could be prevented by the development of such a circulation. This mechanism would tend to accumulate less dense water to the left of the direction of flow, i.e., along the coast. In turn, this would facilitate a lateral, offshore transfer of water, and the contained organisms, at deeper horizons. However, such would not be re-

vealed by the surface sampling of this survey.

A second possibility is that the transfer between the coastal and subantarctic waters proceeds through the agency of discrete pockets of water, formed on a small scale but in an analogous manner, to those between the Gulf Stream and neighboring waters (Iselin and Fuglister, 1948; Ford and Miller, 1952). Isoline configurations in several of the Figures 11-20 suggest the development of pockets on the shoreward side of the north-going oceanic waters. If the transfer of surface water were largely shorewards, as seems possible, it would assist in explaining the abrupt cessation of the offshore occurrences of Coastal species.

The method of the T-S-P diagram is suitable for determining the tolerances of species to temperature and salinity in that it demonstrates their reactions to changes in environmental conditions. The fact that data are collected in the field is advantageous and especially so when considered in conjunction with experimental evidence, for example of the long or short term temperature adaptability of species. Sheard (1953: 21, and personal communication) indicates that temperature tolerances may vary according to the range to which the local stock of a species has become adapted; the occurrences of *Thysanoessa gregaria* in the present survey appear to be a case in point. In general, *Th. gregaria* is rarely captured in subantarctic waters (Sheard, 1953; Boden, 1954). But it was consistently taken as a Southern Subantarctic species during the present survey. It reacted to increasing temperatures (Fig. 6) by a reduction in numbers in a manner similar to other species of the Southern Subantarctic Group. It is possible that this may be a stock of *Th. gregaria* which is adapted to cold water. If so, considerable interest would accrue at this stage in comparing upper and lower temperature tolerances of this and Subtropical stocks, both by experiments and through field data by means of the T-S-P diagram.

The technique of the T-S-P diagram has

been confined to surface waters in this study. It is applicable, however, to determining relationships between plankton and water masses in a vertical direction. David (1955), and others, have been concerned with the

vertical distribution of species on an ocean-wide scale, but the method equally applies to much more limited areas. It should prove of value also in studies of plankton-water relationships near convergences, areas of up-

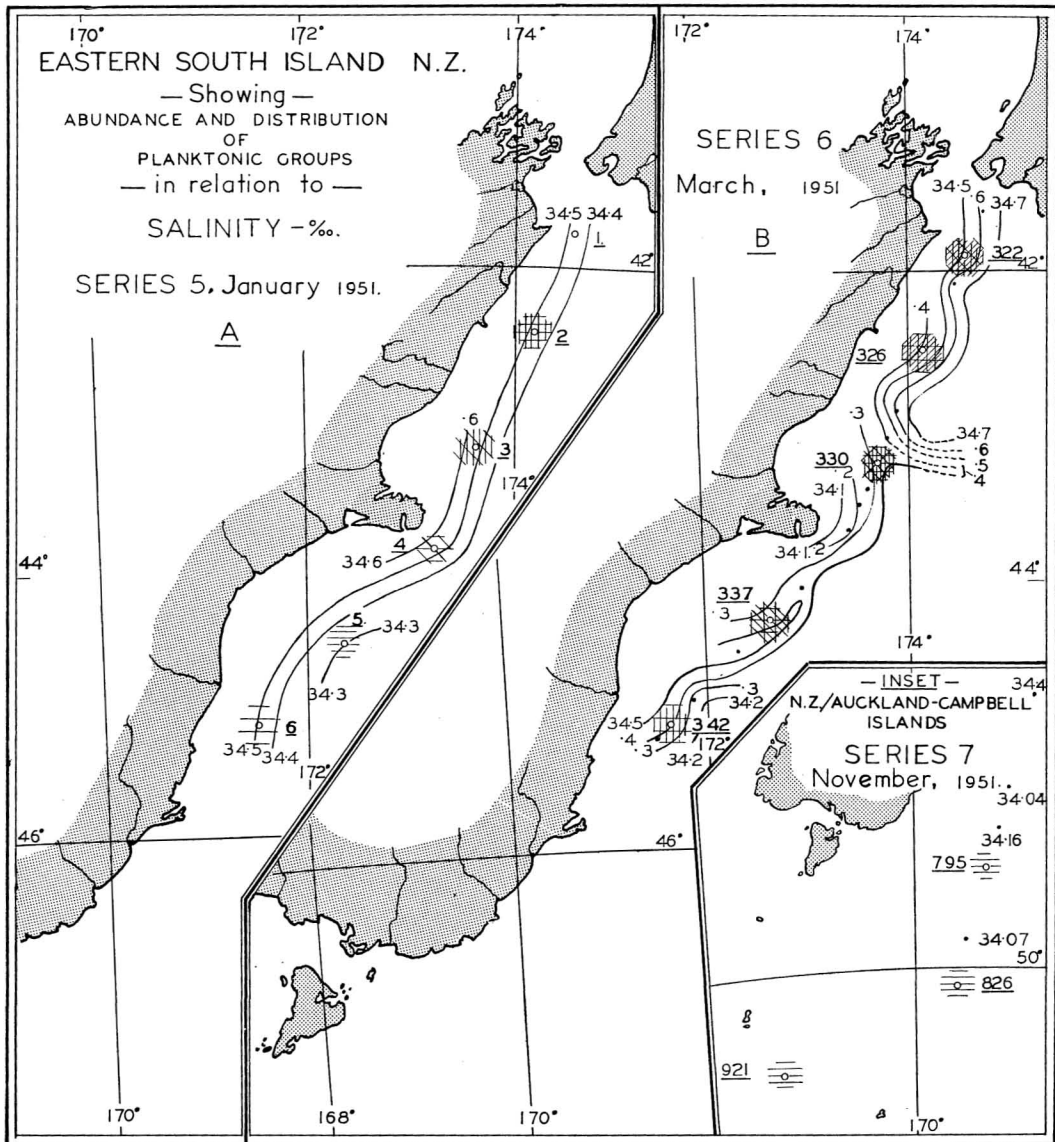


FIG. 20A, B. The distribution of the four planktonic groups in relation to salinity for A. January 1951; Stations 1-6. B. March 1951; Stations 320-343. INSET: November 1951; Stations 795-921.

The position of the subtropical convergence in B is suggested by the dashed isohalines near Station 330. The symbols for the planktonic groups, and the scale of abundance, are as in Figures 10-21.

welling, in water masses surrounding small islands, and it may be of considerable value in the study of patchiness in the distribution of organisms, e.g., of aggregation in the statistical sense. There is little doubt that a comparable technique may be used to determine the effects on organisms of other pairs of environmental factors and in this connection the use by Moore (1950, 1952) and Moore, Owre, Jones, and Dow (1953) of the light and temperature relationships of euphausiids and other zooplankton should not be overlooked. Last, a convenient, three-dimensional picture of the distribution of a species would be presented if a T-S-P diagram, constructed from data from vertical series of samples, were allied with the geographical distribution of the species.

SUMMARY

1. Two principles concerning plankton distribution have been established by earlier workers. First, bodies of water with distinct properties possess distinctive planktonic faunas. Second, when one of these bodies of water mixes with another, the faunas are mixed. In this present study, species have been selected as indicators of the constituent waters of an area about southern New Zealand where waters of subtropical and subantarctic origins are mixing together, and with coastal water. The surface waters entering the area are identified by their temperature-salinity relationships.

2. All occurrences of a number of selected species of the plankton have been superimposed on the T-S diagram of surface waters in the area to produce the temperature-salinity-plankton (T-S-P) diagram. It is found that the distribution of each of the several waters coincides with the distribution of its indigenous species. Further, where one of the waters penetrates into, and mixes with another, it is demonstrated that the species of the one are transported into the other and a mixed fauna results.

3. Examples are discussed in which stations (isolated geographically and in time) aggregate in the T-S diagram. The similar environmental conditions which exist at these stations are the result of several intrusions at different localities of subantarctic into coastal water. The individual intrusions have been demonstrated by considering the geographic distribution of water properties in near-synoptic series of stations. The close affinity between the stations of each aggregate is demonstrated in the T-S-P diagram by means of the similarity of the plankton captured at the stations.

4. Plankton distribution in the T-S-P diagram, allied with that shown by the geographical distribution of the species, has demonstrated a southward migration of the subtropical convergence during the summer.

5. Temperature and salinity tolerances of species and the reactions of species, or groups of species, to changes in temperature and salinity, are readily observable in the T-S-P diagram.

6. The T-S-P diagram is potentially useful in studies of distribution about convergences, small islands, near areas of upwelling, and for studying patchiness of plankton.

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